BEHAVIOURAL AND ECO-PHYSIOLOGICAL STUDIES on BLUE WILDEBEEST (*Connochaetes taurinus*) at the ETOSHA NATIONAL PARK

by H.H. Berry, M.Sc.

Submitted in candidacy for the degree of Ph.D.
University of Cape Town

June 1980

VOLUME I

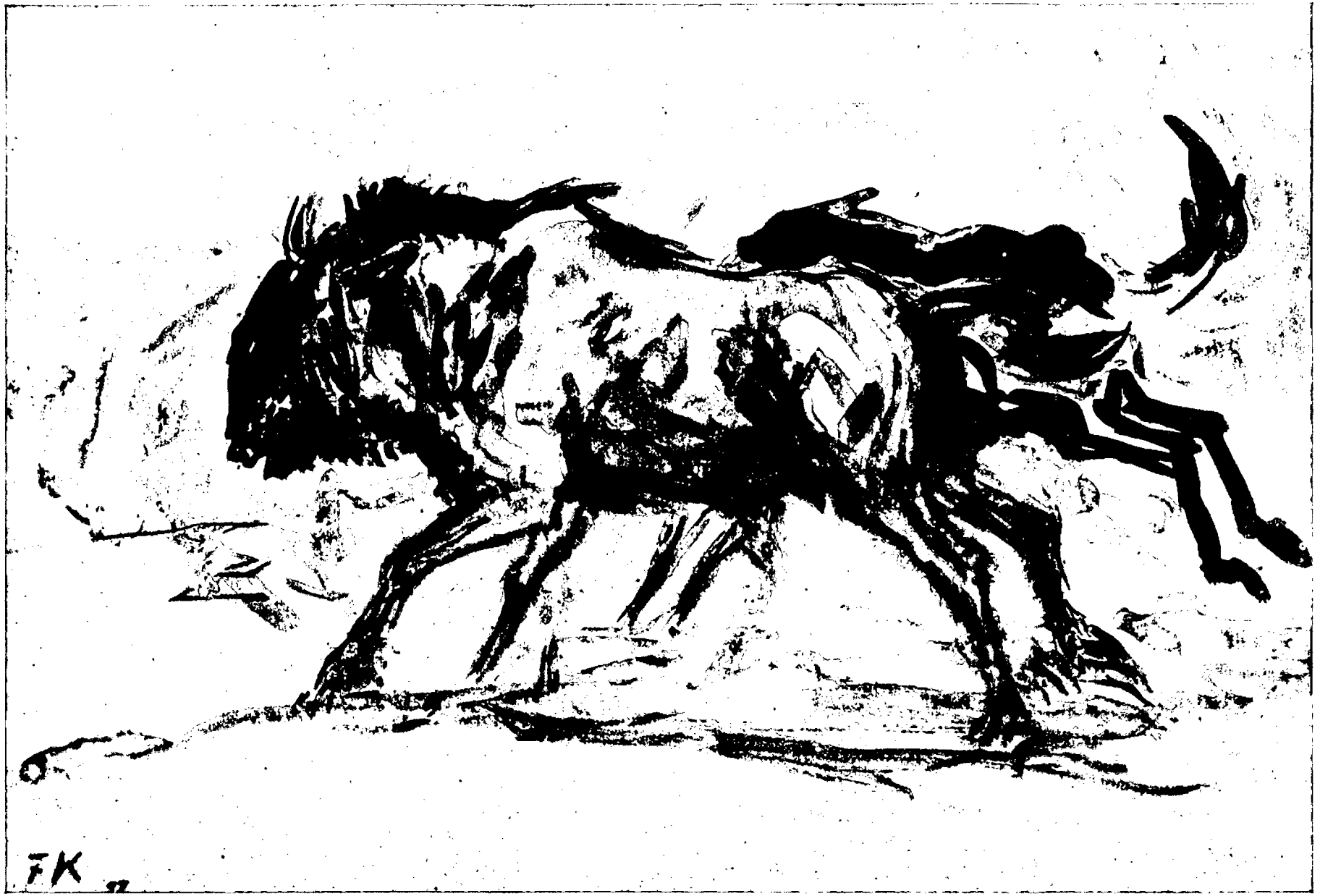
FK

TABLE OF CONTENTS

Page No.

VOLUME I

Page No.

VOLUME II

Page No.

ACKNOWLEDGEMENTS

My study was supervised by Professor G.N. Louw. Professor W.R. Siegfried served as advisor. I thank both of them unreservedly for their interest, their meticulous checking of my progress and the philosophy which they impressed on me. In addition, I am indebted to Professor J. Field and Dr. T. Crowe of the Zoology Department (University of Cape Town) for their advice on computerisation of data and their assistance in obtaining printouts at the computer terminal.

I gratefully acknowledge the South West Africa Administration for permission to use a portion of my official work for this thesis. In particular I thank the Director of Nature Conservation and Tourism, Mr B. de la Bat for suggesting this project and discussing his findings, as former biologist of Etosha, with me. I thank his staff at head office for their logistical support, especially Dr E. Joubert, Mr P. Swart and Mr C. Rochèr. A word of thanks to Miss H. Croeser, for obtaining many of the literature references.

At Etosha, numerous people were involved in providing assistance. I want to single out the following persons :

- Dr J. Hofmeyr and Dr T. van Wyk for immobilisation and

The Assistant Director of Veterinary Services, Windhoek, gave permission for the transport, from Etosha to Cape Town, of blood plasma and specimens taken from wildebeest. The Director of the National Institute for Water Research, C.S.I.R., Pretoria, gave permission to refer to the results of reports. They are thanked for this courtesy.

The pilots and flight engineers of Court Line Helicopters (Pty) Ltd, Cape Town, are thanked for their co-operation during the 1974 aerial census.

The late Mr F. Krampe is acknowledged for the reproduction of his original drawing of wildebeest which is eminently suitable as a frontispiece.

Several persons were involved in the stencilling of draft manuscripts and I thank Mrs Dixon, Mrs Hawthorne, Miss Hoffmann, Mrs Kotze and Mrs van Rooyen for their help. I thank Mrs Jeanette Wood for her masterly typing of the final thesis.

Mr L. Laursen produced the final maps, graphs and figures. I acknowledge his painstaking attention to detail and his absolute accuracy.

My wife, Cornelia, deserves a large share of the credit for the production of this thesis. She transcribed tape

recordings of activity data totalling almost 500 hours onto computer coding sheets, typed the initial manuscript, proof-read the successive drafts and final thesis, assured me during periods of low morale and stood by me unfailingly during the fieldwork and the writing of the manuscript. For these reasons I dedicate this thesis to her.

ABSTRACT

An investigation into the decline of blue wildebeest numbers at Etosha National Park was made during the period 1974-1978. Aspects of wildebeest ecology which were investigated were activity patterns, energy and protein budgets, nutrition, nutritional status, disease and parasites, predators and scavengers, and population structure. Activity patterns in the free-ranging population were measured over a period of one year, using marked individuals and by scanning herds. The population spent, on average, 53 % of its time resting, 33 % grazing, 12 % in movement, 1,5 % in overt social encounters and less than 0,5 % drinking and suckling. Photoperiod and temperature were the primary correlates of activity/inactivity and a linear relationship existed between increasing temperature and increasing inactivity. The activity data were used to calculate an energy budget for maintenance and activity in the population, while energy demand for growth, gestation, lactation and homeothermy were estimated by formulae based on domestic ruminants. Mean increment over resting metabolic rate for free existence in wildebeest approximated 2,0. This represented a mean annual energy demand of 8,5 gigajoules per wildebeest. Similarly, a protein budget was estimated for the population on a seasonal basis. Gestating and lactating cows had the highest protein demand, estimated

to average almost 200 g. day^{-1} per individual. Mean protein demand in wildebeest was 117 g. day^{-1} or 42,6 kg. year^{-1}. Nutritional measurements showed that 97 % of the diet was grass, with feeding selectivity resulting in a wet season peak of 75 % protein-rich grass leaf/sheath. Available protein levels in grass varied from 18 % at sprouting to 4 % at dormancy. Wildebeest are obligate, daily drinkers, making the food-water link critical by limiting them to a foraging radius of 15 km from water. The nutritional balance of wildebeest and their major food competitors was favourable during the study, with sufficient energy and protein produced to meet the demand. Nevertheless, because boundary fences eliminate traditional migration routes, nutrition may be limiting to wildebeest during drought. Nutritional status of wildebeest, as judged by visual rating, kidney fat, bone marrow fat, liver and blood parameters, was good although phosphorus, copper and cobalt may be marginally deficient but not limiting. Furthermore, the mean pregnancy level of 87 % and the high nutritive level of milk were additional criteria for concluding that nutrition was not a limiting factor. Disease, notably anthrax, was considered limiting, resulting in a mean of 62 % of the known mortality in wildebeest. Anthrax and artificial water supplies at Etosha also resulted in predator increases with predator-prey biomass ratios of 1 : 72-105. This was 1,7 times the live mass of predator to prey found in other African conservation

areas. The observed population structure and mortality patterns corroborated the effect of high levels of disease and predation. Calving percentage was normal but 48 % of all adults died between 3 - 6 years of age and at 10 years of age 91 % of all adults had died. A computed demographic model also confirmed that mortality rate exceeded rate of recruitment to the breeding stock. The abnormal levels of disease and predation were consequently considered to be the major causes of the decline of 24 % in wildebeest numbers during 1974 - 1978. Management recommendations to halt this decline include modification of the existing boundaries of Etosha to incorporate previous migration routes, restraint of anthrax, and predator control by closure of artificial water points.

VOLUME I

Section 1

INTRODUCTION

1.1 LITERATURE REVIEW

1.1.1 Historical

1.1.1.1 Discovery, Nomenclature and General Description of Wildebeest Species and Subspecies

Indigenous peoples of Africa, probably the southern African Bushmen and Hottentots, were the first to come into contact with the two wildebeest species. The Hottentots referred to them as "t'gnu" (Dorst and Dandelot, 1970), an onomatopoeic term derived from the animal's nasal snort. The first European discoverers of wildebeest were the early 18th century Boer trekkers who encountered large herds of the animals and named them "wildebeeste", meaning literally "wild cattle". The trekkers distinguished between blue wildebeest or brindled gnu and black wildebeest or white-tailed gnu, the latter being discovered by them during the early 19th century on the highveld plains of South Africa (Lydekker, 1908). The East African wildebeest or white-bearded gnu was first described by Thomas in 1892 (Talbot and Talbot, 1963).

The blue wildebeest *Connochaetes (Gorgon) taurinus taurinus* (Burchell, 1823) has a body mass of 160 - 270 kg and stands 120 - 150 cm at the shoulder. The nominate subspecies was described from a specimen obtained from Bechuanaland (Botswana) by Burchell in 1811 (Sidney, 1965), but according to Ellermann *et al.* (1953) it came from the north-western Cape in 1823. Smithers (1966) and Dorst and Dandelot (1970) give good descriptions of the animal's external features, although the latter authors' inclusion of the words "clumsy appearance" is unfortunate, since the wildebeest is extremely agile, with a well-developed, jinking gallop. In addition, it is worth noting that both sexes have a light brown blaze across the forehead which remains prominent until three years of age. The blaze is a useful guide in age estimation in the field. The East African wildebeest or white-bearded gnu *C. taurinus albojubatus* (Thomas, 1892) differs from the nominate subspecies by being generally lighter in coat colour and the "beard" under the throat is an off-white instead of black (Dorst and Dandelot, 1970).

Although *C.t. albojubatus* and *taurinus* are the best known, the former being far more numerous, three other subspecies exist, namely *mattosi* (Angola wildebeest), *cooksoni* (Cookson's wildebeest) and *johnstoni* (Nyasa wildebeest), according to Allen (1939). However, both Shortridge (1934) and Ellermann *et al.* (1953) regard the subspecies *taurinus* and

mattosi as being synonymous because they are indistinguishable in appearance. The subspecies *cooksoni* and *johnstoni* closely resemble one another in appearance, both having a white chevron blazed across the face. In *cooksoni* the general coat colour is lighter and more grey and the white blaze does not extend below the eyes as it does in *johnstoni* (Sidney, 1965).

The black wildebeest *C. gnou* (Zimmermann, 1780) is smaller in stature (136 - 158 kg) (Von Richter, 1971a) and stands 115 cm at the shoulder (Dorst and Dandelot, 1970). It differs in appearance from *C. taurinus* by the erect tuft of muzzle hairs and forward-curved horns which sweep downwards, curving sharply up and slightly outwards. The long-haired tail, black at the base, with its distal portion white, is the distinguishing feature.

1.1.1.2 Evolution and Pre-History of Wildebeest

The bovids, along with the giraffids, developed from a basic traguloid-pecoran stock which originated in Africa during the late Oligocene (Cooke, 1972). During the subsequent early Miocene a geological development occurred which favoured expansion of the bovids. The African peneplain, more specifically the Kalahari basin, emerged and was less arid than at present. Similarly, there was a widespread uplift of 600 to 1 200 m in eastern and southern Africa

during the late Pliocene which profoundly affected the topography and hence the climate and vegetation (Cooke, 1972). Finally, the extensive latitudinal shifts of climatic belts and ecological conditions which accompanied the glacial and interglacial periods of the Pleistocene, allowed the mammal fauna, which had reached present-day specific status, to move with them. The recent African Quaternary was a period of fluctuating climate with the resultant displacement and isolation of vegetation such as the south-west Arid zone and Somali-Sudanese Arid zones which are biotically very similar (Bigalke, 1972).

The artiodactyls are considered to be the most successful of Africa's endemic mammals, with the Bovidae having no fewer than 78 extant species. Furthermore, the Bovidae have shown remarkable adaptive radiation to fill many of the available herbivorous niches. Bigalke (1972) notes that the Alcelaphini's three genera : *Damaliscus*, *Alcelaphus* and *Connochaetes*, are all grass-savanna animals and that the Tribe is a good example of African endemism. Wildebeest can therefore be considered to have evolved successfully from a bovid stock of African origin whose appearance can be traced back to the early Miocene, a period of 25 million years. Wildebeest in their present-day form appear to have evolved during the Pleistocene (Wells, 1965; Cooke, 1972) and became distributed across Africa during the radical climatic changes of the Quaternary period (Bigalke, 1972).

1.1.2 Recent

1.1.2.1 Distribution, Numbers and General Conservation Status of Wildebeest Species

The distribution of *C. taurinus* (Sidney, 1965) is illustrated in Fig. 1.1. The species shows a distinct preference for open or lightly-wooded savanna throughout its range. The present geographical distribution of *C. taurinus* subspecies, which extends from the equator in east Africa to the south-western portion of the continent (28°S) at the Kalahari Gemsbok National Park, is probably attributable to the "drought corridor" described by Bigalke (1972). This he defines as the area which receives less than 10 mm of rainfall per month in three consecutive months (Fig. 1.1) and suggests that wildebeest are probably very water-dependent. The blue wildebeest *C.t. taurinus* inhabits southern Africa from the Kalahari Gemsbok National Park in the Cape Province, northern South West Africa, southern Angola, western Zambia and eastwards across Botswana, Rhodesia, eastern Transvaal, southern Moćambique, Swaziland and the Mkuzi, Hluhluwe-Umfolozi Game Reserve complex in Natal. Cookson's wildebeest *C.t. cooksoni* is the most limited in distribution, occurring only in the northern Luangwa Game Reserve of Zambia. The Nyasa wildebeest *C.t. johnstoni* was eliminated from its home range in Nyasaland by the end of the 19th century and is now

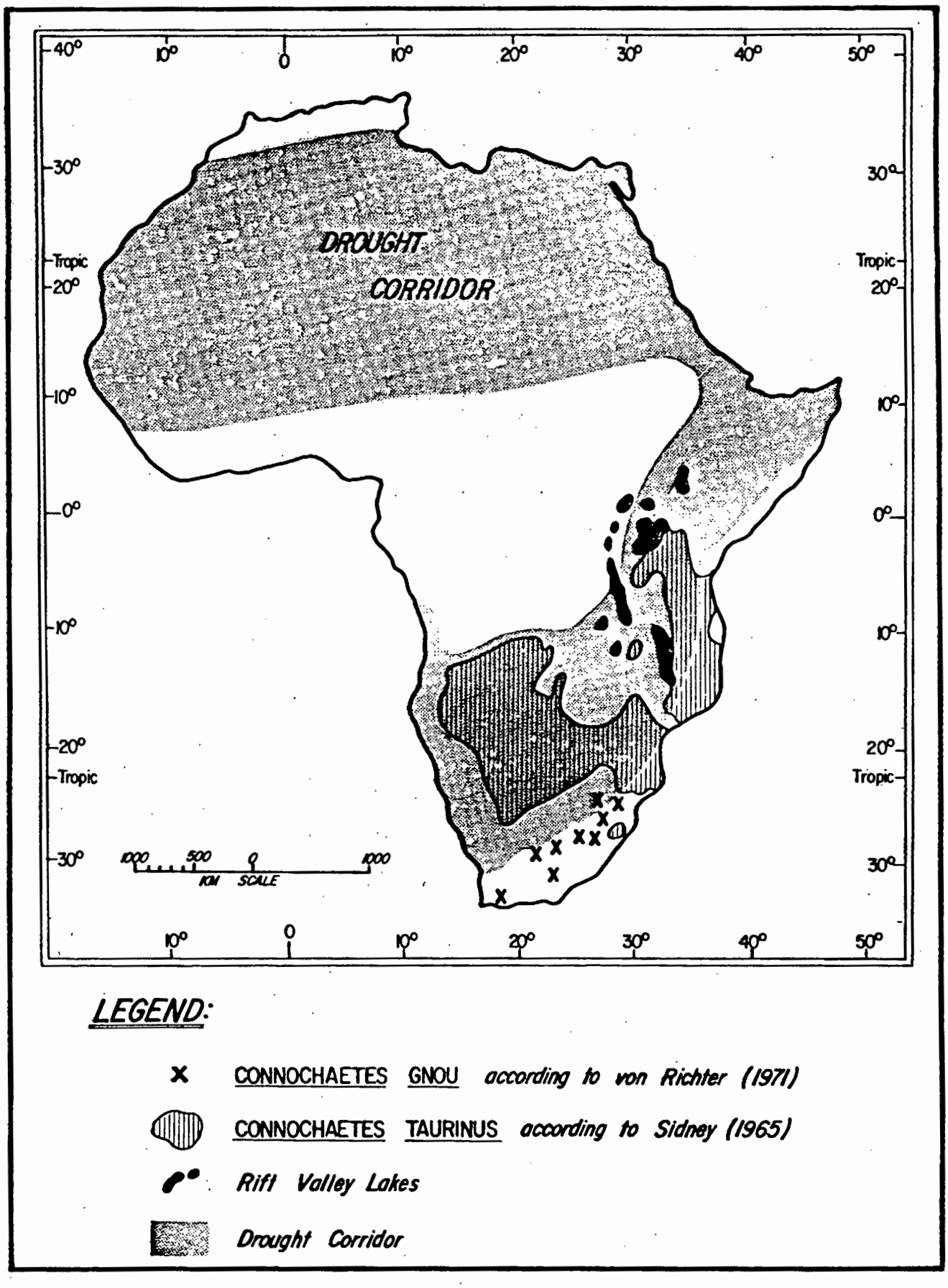

Fig. 1.1 : Distribution of wildebeest in Africa.
The shaded area represents the "drought corridor".

only found north of the Zambesi river in Moćambique, extending into south-eastern Tanzania. However, Smithers (1966) states that *johnstoni* ceased to exist in Nyasaland as recently as 1925. *Connochaetus taurinus albojubatus*, the East African wildebeest, ranges throughout central and northern Tanzania, extending into south-western Kenya.

Numerically, the various populations of *C. taurinus* are still secure in game reserves, but are decreasing sharply in some. On farmland and tribal land the species' status is less certain, with drastic declines known to be occurring. For instance, wildebeest populations of the Etosha National Park as well as the northern tribal lands of South West Africa have experienced a severe decline since 1973 (Berry, 1974-78, Departmental reports). In other regions, however, the wildebeest population has increased. Sinclair (1973a) reported a highly significant increase of wildebeest *C.t. albojubatus* in the Serengeti (263 000 in 1961 to 693 000 in 1971) and a further increase to 1 400 000 in 1977 (Sinclair, 1978, pers.comm.). Nevertheless, the survival of this huge, migratory population is heavily dependent on recognising the Serengeti National Park and its neighbouring tribal lands in Tanzania and Kenya as an indivisible ecological unit (Pennycuick, 1975). Table 1.1 (overleaf) gives the most recent census figures obtainable. No figures were available from Angola, Moćambique and Zambia. Furthermore, wildebeest

TABLE 1.1 : Numerical status of wildebeest *Connochaetes taurinus* in African game reserves and conservation areas. The culling and capture operations in Natal Parks preclude a determination of trend.

Country	Game Reserve (GR) or Protected Area (PA)	Source	Date of census	Estimated population	Trend
Republic of South Africa	Kruger National Park (GR)	National Parks Board of Trustees	1977	4 569	Decline
	Kalahari Gemsbok National Park (GR)	National Parks Board of Trustees	1977	4 000	Static
	Timbavati Private Nature Reserve (GR)	Transvaal Provincial Administration	1977	3 397	Static
	Klaserie Private Nature Reserve (GR)	Transvaal Provincial Administration	1977	3 082	Static
	Hluhluwe - Corridor - Umfolozi Game Reserve Complex (GR)	Natal Parks Board	1976	2 689	-
	M'kuzi Game Reserve (GR)	Natal Parks Board	1973	923	-
	Sabi-Sand Private Nature Reserve (GR)	Transvaal Provincial Administration	1977	508	Decline
	Hans Merensky Nature Reserve (GR)	Transvaal Provincial Administration	1977	120	Increase
	Loskopdam Nature Reserve (GR)	Transvaal Provincial Administration	1977	69	Increase

Table 1.1 (continued)

Country	Game Reserve (GR) or Protected Area (PA)	Source	Date of census	Estimated population	Trend
Swaziland	Hlane Wildlife Sanctuary (PA)	Warden	1976	2 340	Decline
Botswana	Makgadikgadi (PA)	National Parks	1977	60 000	Increase
	Chobe National Park (GR)	National Parks	1977	15 000–20 000	Increase
	Kalahari (PA)	National Parks	1977	280 000	Increase
	Okavango Delta (PA)	National Parks	1977	6 000	Increase
Rhodesia	Wankie National Park (GR)	National Parks	1977	800	Decline
South West Africa	Etosha National Park (GR)	This Study	1978	2 493	Decline
Kenya	Nairobi National Park (GR)	Hillman & Hillman (1977)	1974	8 074	Decline
Tanzania	Serengeti National Park (GR)	Sinclair (1978, pers.comm.)	1977	1 400 000	Increase
Total	-	-	-	±1 800 000	-

on developed farmland were not included in this survey.

Free-living populations of *C. gnou* are at present restricted to South Africa and have apparently always been confined to the southern savanna. Historically there appears to have been only a very narrow zone of overlap in the distribution of *C. gnou* and *C. taurinus*. The former species characteristically inhabits open, treeless Karoo and Highveld while the latter prefers more wooded savanna. It is therefore of interest, as noted by Bigalke (1972), that in the absence of *C. gnou*, *C. taurinus* inhabits both open grassland such as the treeless plains surrounding the Etosha Pan and the wooded savanna of northern South West Africa. Guggisberg (1970) gave a total of only 300 *C. gnou* counted in 1938. In 1945 a survey showed a population of at least 1 048 (Bigalke, 1947) and Brand (1965) obtained a total of 1 808 black wildebeest. However, Guggisberg (1970) gave a figure of 2 117 for 1965. Von Richter (1971a) undertook a third major survey of the species, locating 3 120 animals. He gave their distribution as 1 944 (Orange Free State), 508 (Cape Province), 494 (Transvaal) and 174 (Natal). Von Richter (1971a) regarded this significant increase in numbers as being largely due to the restocking of game reserves and farms. Because of this the species is classified as "rare, but secure" in Von Richter's (1974) list. Fig. 1.1 shows the distribution of *C. gnou*

according to Von Richter (1971a).

1.1.2.2 The Decline and Present Conservation Status of Blue Wildebeest in South West Africa

The first estimate of the blue wildebeest population which could be traced from South West Africa (SWA) was in 1912 when Fischer (1914) gave the number occurring in the Kalahari districts (eastern SWA) as 5 190. The earliest census of large animals in SWA was undertaken in 1926 when the Secretary for the Territory instructed all magistrates and officers in charge of tribal lands to submit a report on the status of wildlife. The survey included 17 magisterial districts plus Owamboland and Etosha. (Estimates obtained in the Grootfontein district were inaccurate, the wildebeest being described as "fairly numerous". Similarly, in the Rehoboth district the census was unsuccessful.) Therefore, figures are only available for 15 districts of which five reported that wildebeest were present. These were : Gobabis (3 200), Gibeon (2 000), Aroab (600), Otjiwarongo (300) and Okahandja (17). Thus 6 017 wildebeest were estimated to be present on European farms and 17 500 in the Etosha-Owambo area, giving a total of 23 517 wildebeest in SWA in 1926 (Fig. 1.2).

Several censuses of game in SWA were undertaken after 1926

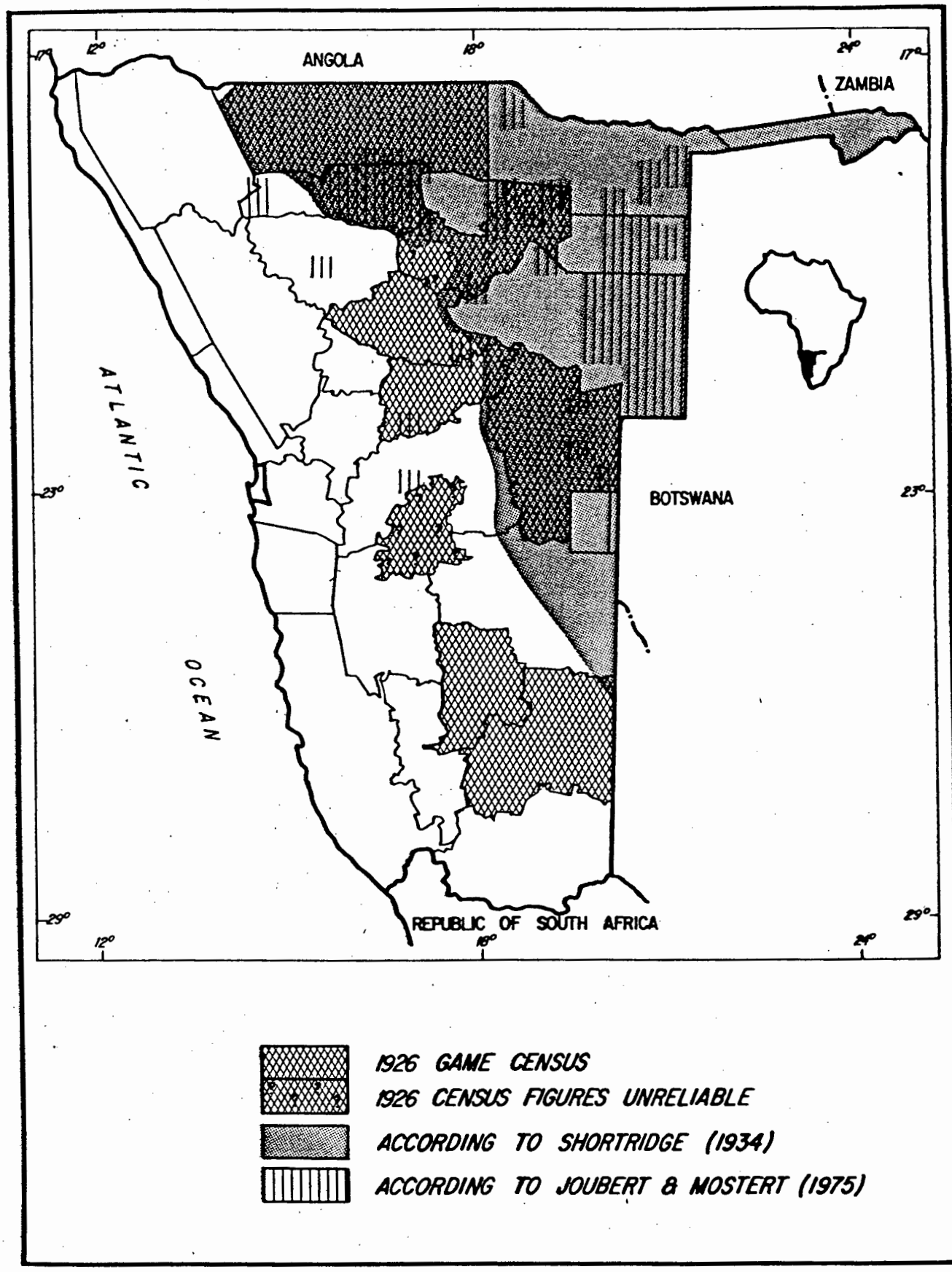

Fig. 1.2 : Past and present distribution of blue wildebeest in South West Africa.

but none of them gave quantified information on wildebeest (Joubert and Mostert, 1975). Shortridge (1934) however, considered wildebeest to be ". . . the most plentiful of large open-country antelope . . ." Joubert and Mostert (1975) undertook a comprehensive survey on the distribution and status of some mammals in SWA. Apart from 3 717 wildebeest counted in Etosha by Joubert *et al.* (1973), Joubert and Mostert (1975) found that 245 wildebeest occurred on farmland (Fig. 1.2) and considered that "it is extremely doubtful whether there are more than 500 individuals in the rest of South West Africa". They concluded that the wildebeest's survival in SWA seems to be endangered.

There appears to be little doubt that wildebeest were the most numerous of the large ungulates in SWA during the early 20th century. For example, Jaeger (1926-7) reported that between 20 000 and 30 000 wildebeest were present on the Etosha plains in 1913. The species may have retained this numerical status until as recently as 1960 (Section 2.6) when "game-proof" fences were erected over large areas in the northern part of the territory. This resulted in a relatively small percentage of the previous, migratory population (probably not more than 4 000) being afforded adequate protection within the Etosha National Park when its fencing was completed in 1973 (Ebedes, 1977, pers.comm.). Wildebeest excluded from Etosha have been decimated to the

point where only isolated herds remain and the species can be considered in danger of disappearing completely from the farming areas and tribal lands of SWA. Within Etosha the wildebeest population has declined by a further 33 % since 1973 and stood at *ca.* 2 500 in 1978 (Berry, 1978, Dept. report).

The present study was consequently undertaken to establish reasons for the continued decline in the wildebeest population within the present-day Etosha National Park, and to formulate management plans which may assist in retaining a viable population at Etosha.

1.1.2.3 Recent Research

Wildebeest have received considerable attention, firstly as a result of exploitation and later through scientific research, in Africa. Early man presumably had little effect on the species (Klein, 1979). However, the introduction of modern weaponry took a heavy toll and the insiduous pressures of agricultural and other developments have increased more during the past few decades than in the entire previous history of Africa (Guggisberg, 1970). It is likely that a conspicuously large ungulate, such as the wildebeest, which characteristically prefers open plains and savanna, would be among the first species to be

exploited by modern humans. Although game reserves were proclaimed concurrently with this development, they were not planned with ecological considerations in mind and consequently their boundaries are mostly artificial. It is only during the past two decades that serious ecological investigations have been conducted in natural African systems.

One of the first modern scientific investigations on wildebeest in relation to their habitat occurred in 1958 when Grzimek and Grzimek (1960a, b) undertook an aerial census of the plains animals in Serengeti National Park, Tanganyika (Tanzania). This was subsequent to the Pearsall report (1957) which recommended the reduction of the Park. They found that white-bearded wildebeest *C. taurinus albojubatus* were the most numerous large mammals (99 481 out of 366 980 animals counted, or 27 %). Between 1956 - 1962 Talbot and Talbot (1963) undertook a series of research expeditions to East Africa totalling 34 months and culminating in the publication of the first ecological monograph on wildebeest, specifically in western Masailand, which incorporates the Serengeti-Mara Plains of Tanzania and Kenya. In this period Fraser-Darling (1960) also carried out an investigation on the Mara Plains. He spent three months in the field in 1958 and published a broad account of the habits and movements of the animals, recognising that a study of the

wildebeest would lead to a better understanding of the wild animal complex on the plains.

The earlier work on wildebeest in East Africa was followed by a detailed study of its population ecology by Watson (1965a, b; 1966; 1967; 1969a, b) which is probably one of the most comprehensive investigations undertaken on the species to date (see also Watson and Kerfoot (1964)). During the same period Estes (1966, 1968, 1969) studied the behaviour and life history of wildebeest, giving specific attention to the territorial behaviour of bulls. Further reference to this work is to be found in Estes (1974, 1976). Other major research, which described the grazing system in Serengeti National Park by ungulates, included the wildebeest as an important component and resulted in the building of a predictive model (Bell 1969, 1971; Gwynne and Bell, 1968). The feeding interaction between wildebeest and zebra on the Athi-Kaputei Plains, a semi-arid region of Kenya, was studied by Owaga (1975) and Pennycuick (1975) described wildebeest migrations in the Serengeti from 1960 to 1975. Recently, Inglis (1976) traced the wet season movements of individual, migratory Serengeti wildebeest using radio transmitters attached to 16 animals.

In southern Africa the blue wildebeest *C. taurinus taurinus* featured prominently in a study of ungulate-habitat

relationships by Hirst (1975) which included an estimate of the energy flow to ungulate populations in the lowveld savanna region of eastern Transvaal. Workers in the adjoining Kruger National Park designed a model for predicting population trends in wildebeest (Starfield *et al.*, 1976). This model was constructed from earlier data collected by Braack (1973) and Smuts (1975). More recently, Attwell (1977) investigated the reproduction and population ecology of wildebeest in Zululand, Natal.

Specialised work on the use of energy by wildebeest in East Africa was done by Rogerson (1966, 1968) and its thermoregulatory ability by panting was investigated by Taylor *et al.* (1969). In a study of the diet of wildebeest and other wild herbivores, Casebeer and Koss (1970) found wildebeest to be less selective in the grass species they grazed than domestic cattle and that in the rainy season they favoured the three most available species in Kenya's Masailand. Some characteristics of wildebeest habitat selection in East Africa in relation to calcium and lactation are available in a preliminary report by Kreulen (1975). In a separate study, Cooper *et al.* (1975) found that there was considerable variation in the serum proteins of wildebeest compared to other ungulates in a free-living state in Botswana. The water requirements of wildebeest and other herbivores inhabiting the semi-arid Amboseli

savanna ecosystem in the south of Kenya are well documented by Western (1975), who found that water-dependent species, including wildebeest, are mainly grazers, while the water-independent components of the community are almost exclusively browsers. In a comparative study on the rumen physiology of wildebeest, other wild ungulates and cattle in East Africa, Hoppe *et al.* (1977) demonstrated that the wild herbivores selected green grass when it was available while cattle were more catholic in their diet. An interesting paper by Sinclair (1977a) presents strong evidence linking the lunar cycle and timing of conception in Serengeti wildebeest, which is the first such definite relationship reported for mammals.

In the veterinary field a live vaccine developed from a strain of the protozoan *Besnoitia besnoiti*, causing "elephant skin disease", was successfully used to immunise cattle after its discovery in wildebeest from the Kruger National Park (Bigalke *et al.*, 1967). It was also found that wildebeest in arid regions carried remarkably low ectoparasite loads, even when in poor condition, when carcases were examined immediately after death in the Kalahari desert (Child, 1972a). The ecology of anthrax *Bacillus anthracis* was the subject of intensive study by Ebedes (1976a, b) in Etosha National Park, where wildebeest (35 % of all anthrax-infected carcases) were second only to

zebra (54 %) in susceptibility. Veterinary drugs have been successfully used in the immobilisation of wildebeest in the free-living state and capture methods have reached a sophisticated stage (Orr and Moore-Gilbert, 1964; Harthoorn and Bligh, 1965; Pienaar *et al.*, 1966; Pienaar, 1973; Ebedes *et al.*, 1977; and Hofmeyr, 1977, pers.comm.).

There are several very useful publications regarding field censuses of wildebeest. For instance, to achieve accuracy in counting the estimated 750 000 migratory wildebeest in the Serengeti, Norton-Griffiths (1973, 1974, 1978) developed a method of vertical aerial photography to sub-sample randomly located transects of the herds. Sinclair (1973a) analysed in detail the errors inherent in the counting techniques employed by various researchers of Serengeti wildebeest since 1958. Some earlier papers on wildebeest counts are also useful, *vide* Stewart and Talbot (1962), Talbot and Stewart (1964), Turner and Watson (1964), Watson (1969b), Watson *et al.* (1969).

Several other publications on wildebeest in the remainder of southern Africa which are relevant to this study are Dasmann and Mossman's (1962a, b) findings on reproduction rate and population structure in Rhodesia and Eloff's (1959, 1961, 1962, 1966) observations on migration, habitat and range extension of wildebeest in the Kalahari Gemsbok

National Park. In addition, Pienaar's (1963) records of wildebeest abundance and proliferation in the Kruger National Park were referred to and Du Plessis' (1969) report on past and present distribution of Perissodactyla-Artiodactyla in southern Africa confirmed the previous ubiquity of wildebeest in suitable habitat. In the Natal Parks, Hitchins (1966) recorded body mass of wildebeest and Bourquin *et al.* (1971) reviewed the species' status, while Mentis (1970) estimated the biomass of wildebeest in the Umfolozi Game Reserve. In a separate paper, Mentis (1972) summarised the sex ratios and reproductive data of wildebeest from major African populations.

Although formerly one of the most abundant ungulates in East Africa (Petrides, 1956; Swynnerton, 1958) and southern Africa (Estes, 1968), recent publications indicate a significant decline in wildebeest numbers in the latter region. Child (1972b) reported a die-off involving several thousand wildebeest in Botswana, following drought conditions. Bachmann as reported by Child (1972b) estimated that 15 000 wildebeest died within a four-month period in that country in 1964. Starfield *et al.* (1976) and Smuts (1978c) have quantitative data from the Kruger National Park showing that wildebeest declined from 14 000 in 1969 to 4 600 in 1977. The present study will detail similar trends in Etosha National Park. Von Richter (1974),

however, did not consider blue wildebeest to be an endangered species in his survey of the existing conservation areas in southern Africa. In East Africa, Hillman and Hillman (1977) also found that drought conditions increased wildebeest mortality in Nairobi National Park, where 767 carcases (10 % of the population) were recorded. In sharp contrast to these publications, the paper by Sinclair (1973a) showed a considerable increase in the wildebeest population of Serengeti from *ca.* 263 000 (1961) to *ca.* 692 000 (1971). This population has since more than doubled and was estimated to be 1 400 000 in 1977 (±400 000 with 95 % confidence limits) (Sinclair, 1978, pers.comm.). The highly complex interactions between ecological factors which may have given rise to this situation are described by Sinclair (1973b, 1974).

Mention should also be made of the impressive East African studies of predator impact on wildebeest and other plains fauna by Wright (1960), Guggisberg (1961), Bouliere (1963, 1965), Adamson (1964), Estes (1967), Kruuk and Turner (1967), Makacha and Schaller (1969), Kruuk (1966, 1972, 1976), Schaller (1972) and Rudnai (1974). In South Africa, similar, relevant studies on predators have been undertaken by Eloff (1964, 1973a, b, 1975), Hirst (1969), Pienaar (1969), Steele (1970), Von Richter (1972b), Bearder (1975), Starfield *et al.* (1976), Smuts (1975, 1976, 1978a, b, c) and Smuts *et al.* (1978).

Due to its international status as a previously endangered species, the black wildebeest *C. gnou*, which is now retained on the list of "rare, but secure" animals in South Africa (Von Richter, 1974), has received special attention. Bigalke (1947) and Brand (1965) carried out the first censuses and Von Richter (1971a, b, 1972a) studied this species' biology and territorial behaviour in detail. Walther (1966) analysed the social ethology of black wildebeest in relation to recumbancy and rising, using captive animals. In a review of milk analyses of wild animals, A. Smith (1970) compared the milk of black wildebeest with that of other herbivores and found that all constituents were on a par with those of other ungulates. Skinner *et al.* (1974) included black wildebeest in their study of seasonal effects on the breeding cycle of antelope of the western Transvaal highveld. They classified the species as exhibiting a clearly defined breeding season.

The past distribution of wildebeest and their present geographical status is contained in a resumé by Sidney (1965) who concluded that black wildebeest had increased numerically over the past 50 years, but that *C. taurinus* had decreased in range considerably during the same period, having disappeared entirely from Nyasaland (Malawi). Moreover, in all African countries, notably South Africa, Bechuanaland (Botswana), Northern Rhodesia (Zambia) and

Moçambique, Sidney (1965) gave evidence of a greatly reduced range, mostly as a result of agricultural development.

The taxonomy of wildebeest has undergone considerable modification. Classification for the present study is based on Ellermann *et al.* (1953) who reviewed southern Africa's mammals and, in particular, the genus *Connochaetes* from 1812 onwards. For reference to *C. taurinus* subspecies outside the study area, Allen's (1939) checklist of African mammals has been used.

A search of the early literature provided numerous miscellaneous publications on wildebeest. The more important references relating to South West Africa are Fischer (1914) and Shortridge (1926-7, 1934). In South Africa, Roberts' (1951) classical work and that of Stevenson-Hamilton (1947) gave the best descriptions of wildebeest. One notable investigation which included wildebeest, was Pocock's (1910) treatise on the specialised cutaneous glands of ruminants. In addition, various field guides are available which provide biometric and life history data on wildebeest. Those consulted were Smithers (1966, 1971), Dorst and Dandelot (1970) and Zaloumis and Cross (1974).

To summarise, wildebeest *C. taurinus* have formed the

subject of four major investigations. They were : Talbot and Talbot's (1963) ecological monograph on the subspecies *albojubatus* in western Masailand, Watson's (1967) investigation into its population ecology in the Serengeti, and Estes' (1968) study of the territorial behaviour of *albojubatus* in Ngorongoro crater. In southern Africa, the reproduction and population ecology of the subspecies *taurinus* in Zululand was investigated by Attwell (1977). Apart from the ethological study of *albojubatus* by Estes (1968), the remaining three major investigations of wildebeest were all directed at solving management problems in game reserves. It is of interest that one of these reports (Watson, 1967) dealt with a rapidly increasing population of *albojubatus*; partly the result of the acquisition of immunity against rinderpest virus.

These major research projects on wildebeest have dealt with the behavioural, reproductive and demographic aspects of the species' biology in considerable depth. However, no detailed study of the activity patterns (as distinct from social and ethological characteristics) of free-living wildebeest has yet been undertaken. Furthermore, it has not yet been possible to compose an energy budget for the species in the wild, based on quantitative data. One of the major aims of the present study was to provide such a data base.

1.2 OBJECTIVES OF THE STUDY

The apparent sharp reduction in the number of blue wildebeest at Etosha National Park, following its fencing (Section 2.6), provided sufficient reason to undertake research directed at identification of the causes responsible for the local population's decline. The primary aim of my investigation was therefore to establish which of the major environmental factors such as food, water, climate, disease and predation may have become limiting to Etosha's wildebeest and then to make recommendations for management practices to halt and possibly reverse this decline.

Section 2

STUDY AREA

2.1 LOCATION AND AREA

The study was conducted within the Etosha National Park, South West Africa-Namibia, a reserve proclaimed for the protection of fauna and flora. I will hereafter refer to the reserve as Etosha. Its co-ordinates centre at $19^{o}S$ $16^{o}E$ (Fig. 2.1) and it encompasses an area of 22 270 km^2. Etosha extends 295 km east-west with a north-south variation of 65 - 110 km. One of its major physical features is the vast salt-pan desert, namely the Etosha Pan, which occupies 4 590 km^2 of the eastern sector. Its area, together with that of adjacent, smaller salt-pans (550 km^2), combines to give a total of 5 140 km^2 or 23 % of Etosha which comprises a largely barren area.

2.2 PHYSIOGRAPHY

2.2.1 Geology

The main geological features of Etosha have been described

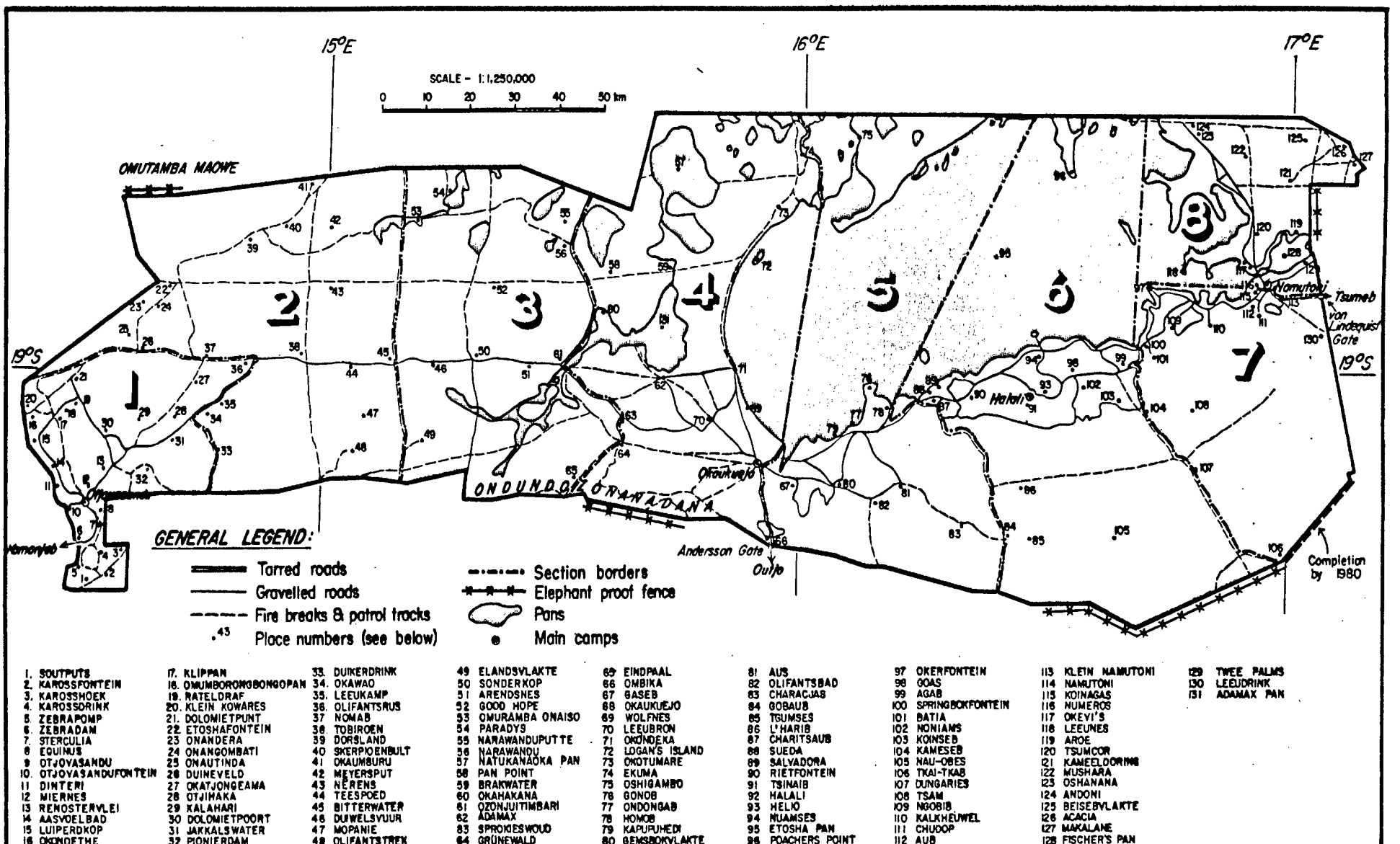

Fig. 2.1 : Map of Etosha National Park, South West Africa, giving boundary fences, place names, roads, water points and the eight sub-divisions used by nature conservators

by Jaeger (1926-7) and Wellington (1938, 1955). The Kalahari Basin is regarded as a major physiographic region of southern Africa, being divided on hydrographic grounds into three sub-regions : the Etosha Basin, the northern Kalahari and the southern Kalahari (Wellington, 1955). The geological map of Etosha (Fig. 2.2) shows that 85 % of its area is composed of calcareous sand and gravel (the so-called "Kalahari beds"), exceeding 50 m in depth. The remainder of Etosha, especially the south-western and far southern areas is made up of dolomite and limestone outcrops of the Otavi series, Damara system, which intrude from the south and south-east. Other minor formations in Etosha which occur adjacent to the Otavi series are the Mulden series of quartzite, slate and conglomerate; the Nosib formation of phyllite and conglomerate; the Khoabendes formation of porphyry and felsite and the Archean complex of granite and gneiss. Separately, to the north of the Etosha Pan, there is a very small intrusion of the Ecca series, Karoo system, composed of Kalahari sand overlying shale and sandstone.

The ecological significance of these geological formations is that the calcareous beds provide for drainage of water into the Etosha Pan, especially along its southern shores, where numerous so-called "contact" fountains flow. These fountains are the preferred drinking places for wildebeest during the dry season. Furthermore, the alkaline and saline

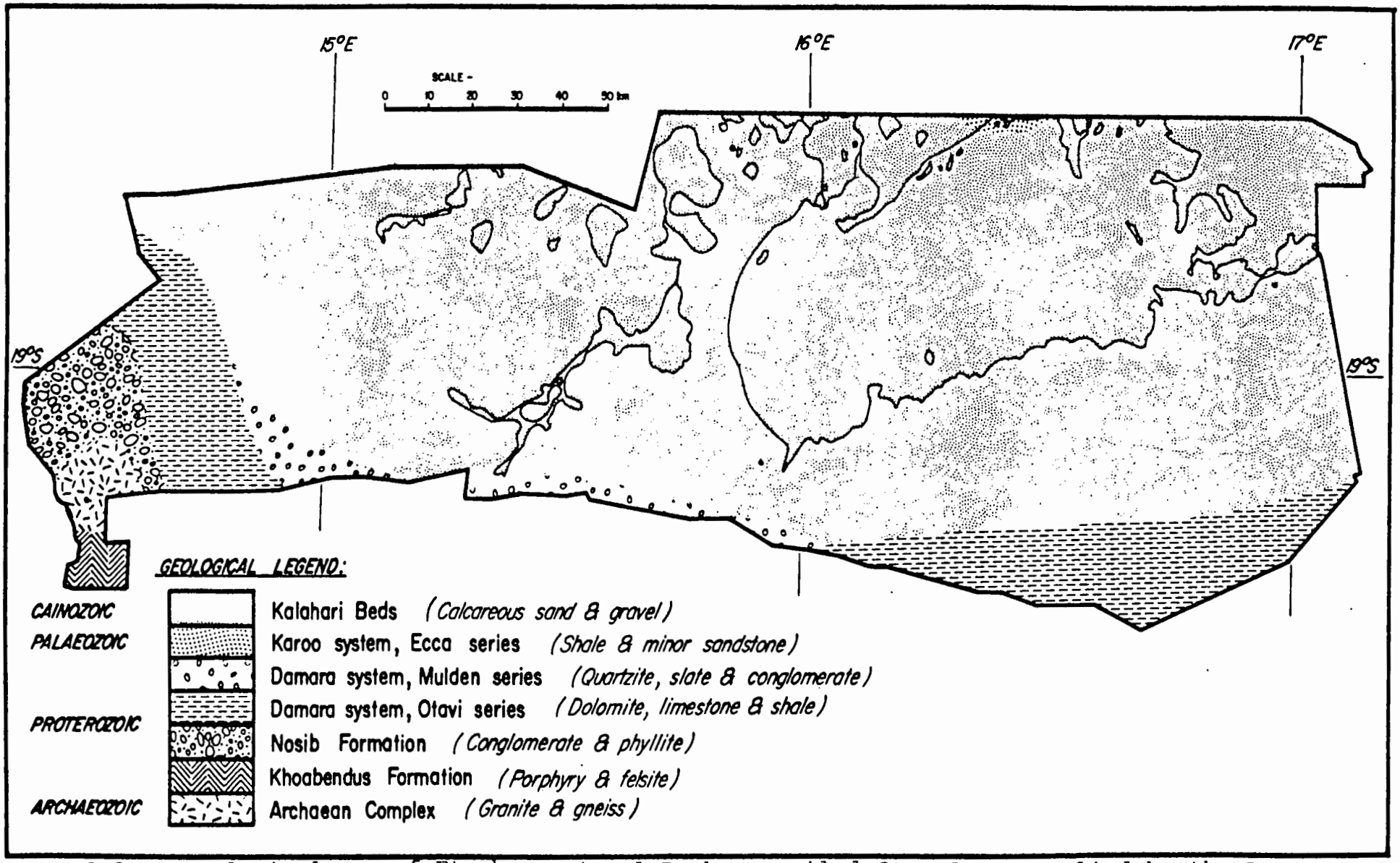

Fig. 2.2 : Geological map of Etosha National Park, compiled from data supplied by the Department of Mines, Geological Survey Office, Windhoek.

nature of the soil surrounding the Pan limits vegetation to hardy, halophytic grasses and shrubs, interspersed with thorn thickets. This grassland is favoured habitat for wildebeest.

2.2.2 Pedology

For the purpose of investigating the relationship between soils and plants in Etosha, Le Roux and Verster (1974, unpubl. report) divided the area into seven major regions (Fig. 2.3), although localised overlays of various soils intrude, obscuring the main features. The Etosha Pan was not included in their series of soil sampling sites and profile pits. The following description is based largely on their findings and on my observations during aerial surveys. I will relate these major pedological regions to the vegetation and its habitation by wildebeest (Section 2.3).

2.2.2.1 Saline Pan Desert

The Etosha Pan, together with adjacent, smaller salt-pans which are situated mostly to the west of it, is composed largely of clay, silt and fine to coarse sand in the ratio 3:5:2 (Berry, 1972). In pre-historic times the Kunene River, now situated 220 km north-west of Etosha Pan at its

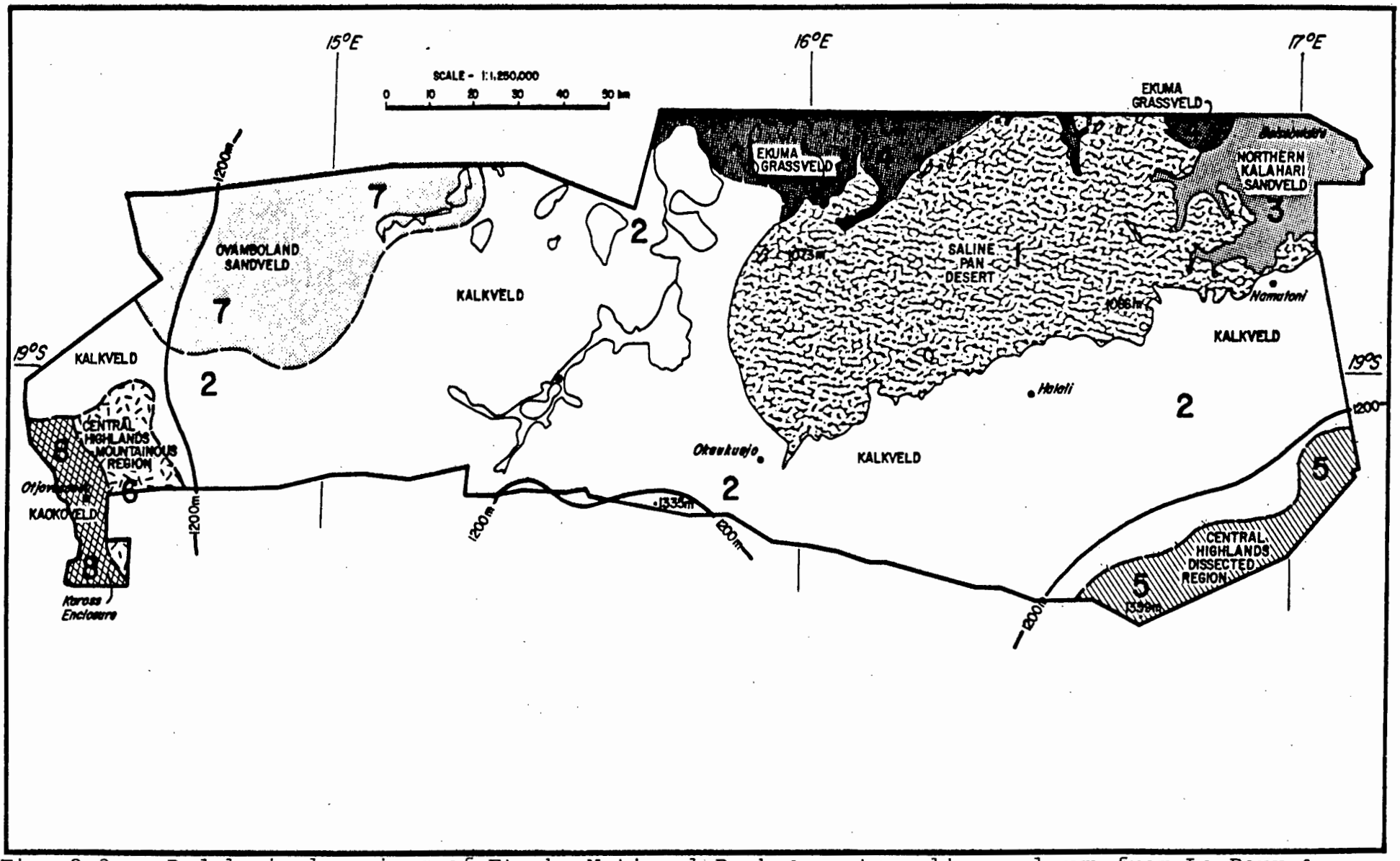

Fig. 2.3 : Pedological regions of Etosha National Park & contour lines, drawn from Le Roux & Verster (1974) & the topographical map published by the Surveyor-General, Windhoek (1978).

nearest point, flowed towards the latter along the Etaka-Nepoko-Ekuma Oshanas or waterways (Wellington, 1938). However, a process of "river piracy" (the capture of a slow stream by a faster stream lying transverse to it, which changes the direction of flow) is in progress (Wellington, 1938). Unless natural erosion is interfered with, the present-day drainage of the Ekuma river into the Etosha Pan may be diverted back into the Kunene river. The latter has cut back in a northerly direction, away from its former direction of flow towards Etosha Pan and now flows into the Atlantic Ocean. From this it is clear that the Etosha Pan formerly received more water than at present and that it may eventually lose the major part of its drainage from the north. The Etosha Pan is virtually flat, with a difference of 13 m in altitude between its eastern and western edges, a distance of 125 km (gradient 1:9 600) (Surveyor-General's Report, 1975).

2.2.2.2 Kalkveld

This region covers the greatest area (50 - 60 %) of Etosha's surface, extending from east to west in a broad band from Namutoni along the southern shore of the Etosha Pan and continuing from its western side to Otjovasandu (Fig. 2.3). It is composed of greyish-brown, sandy clay loams to black clay with recurrent, low outcrops of calcareous rock in the

eastern half and shallow, weakly formed black clay pans in the west. In profile the eastern Kalkveld of Etosha is continuously undulating with a mosaic of interconnected, poorly developed drainage lines. The western Kalkveld is less uneven and for the greater part it is a flat to gently undulating plain, interspersed with small pans.

2.2.2.3 Northern Kalahari Sandveld

This portion of Etosha is limited to the north-eastern corner. It is composed of yellowish-brown sand of a medium texture, with isolated patches of grey sandy loams. Characteristically it is a flat plain with isolated pans which have either formed, such as Beiseb (Fig. 2.3), or are in the process of forming.

2.2.2.4 Ekuma Grassveld

A narrow band of moderately deep to deep (0,5 m to more than 1 m) loamy sand adjoins the Northern Kalahari Sandveld. It extends westward, fringing the north of Etosha Pan to the Natukanaoka Pan, which is the second largest pan in Etosha. The Ekuma Grassland's landform is flat (such as the Andoni plain) to slightly undulating, or terraced in the vicinity of the Ekuma river.

2.2.2.5 Central Highlands Dissected Region

Limited to the far south-eastern corner of Etosha, this minor region is mainly rock, interspersed with shallow and stony, sandy loams. The low-lying areas have accumulated a veneer of black clay soils. It is a hilly to moderately mountainous area with some valleys.

2.2.2.6 Central Highlands Mountainous Region

The transitional zone between Etosha's Kalkveld and the Kaokoveld lies in the south-western corner. It is the smallest, distinct region of Etosha, with strong outcrops of weathered granite surrounded by very shallow to deeper, grey loamy to red sandy soils. The outcrops of granite rise sharply from the flat plains to the east and merge in the west with the hilly Kaokoveld.

2.2.2.7 Ovamboland Sandveld

Confined to the north-western parts of Etosha, this region exhibits a thin veneer of reddish-brown sand which overlies the calcareous beds. There are accumulations of grey sandy loams which form in the low-lying washes. The area is undulating and low ridges of sand dune are discernible from an aircraft.

2.2.2.8 Kaokoveld

The extreme south-western part of Etosha, namely the Kaross enclosure (Fig. 2.3) can be considered as an example of Kaokoveld. Weathered granite outcrops intermingle with washes of coarse, reddish sand and in the valleys the soil's texture changes to a sandy loam. The physical appearance is hilly, with rocky screes in evidence and drainage lines are well-defined. Sandy, seasonally dry washes create a riverine effect in the valleys.

2.2.3 Altitude

Etosha lies between the 1 000 m and 1 400 m contour lines (Fig. 2.3) with its greatest area within the 1 000 m to 1 200 m contours. The highest points are found on the southern boundary at Ondundozonanandana hills (1 335 m) and in the Central Highlands Dissected Region (1 359 m) where the elevations are 200 m above the surrounding Kalkveld. The Etosha Pan has the lowest elevation, with a point 1 073 m in the north-western corner near the Ekuma river mouth. The Pan's greatest elevation is in the south-west near Okerfontein (1 086 m). Thus there is a maximum difference of only 13 m over an area of 4 590 km^2 and for most parts the Etosha Pan averages 1 080 m in altitude.

2.2.4 Climate

The study area is situated in the Arid Savanna Biome, which is characterised by annual isohyetal limits of 150 - 600 mm (Tinley, 1975). Weather data relating to Etosha were obtained from rainfall measurements made discontinuously since 1901 at Okaukuejo and 1902 at Namutoni. In addition, rainfall measurements were made at Andersson Gate since 1965 and at Halali and Otjovasandu since 1966 (refer Fig. 2.4 and Weather Office records, Windhoek). In May 1974, when the present study began, I arranged for the erection of a First Order weather station at Okaukuejo by the Weather Office, Windhoek. Since then, continuous, daily synoptic weather readings have been recorded at 08h00, 14h00 and 20h00. This weather station is centrally situated to the study area and most of the observations on wildebeest were made within a radius of 50 km of it.

Since it is impracticable to distinguish between the four traditional seasons at Etosha, I have followed the method suggested by Walter (1973). Three identifiable climatic periods have been arbitrarily allocated, namely :

wet and hot (1 January to 30 April)
dry and cold (1 May to 31 August)
dry and hot (1 September to 31 December).

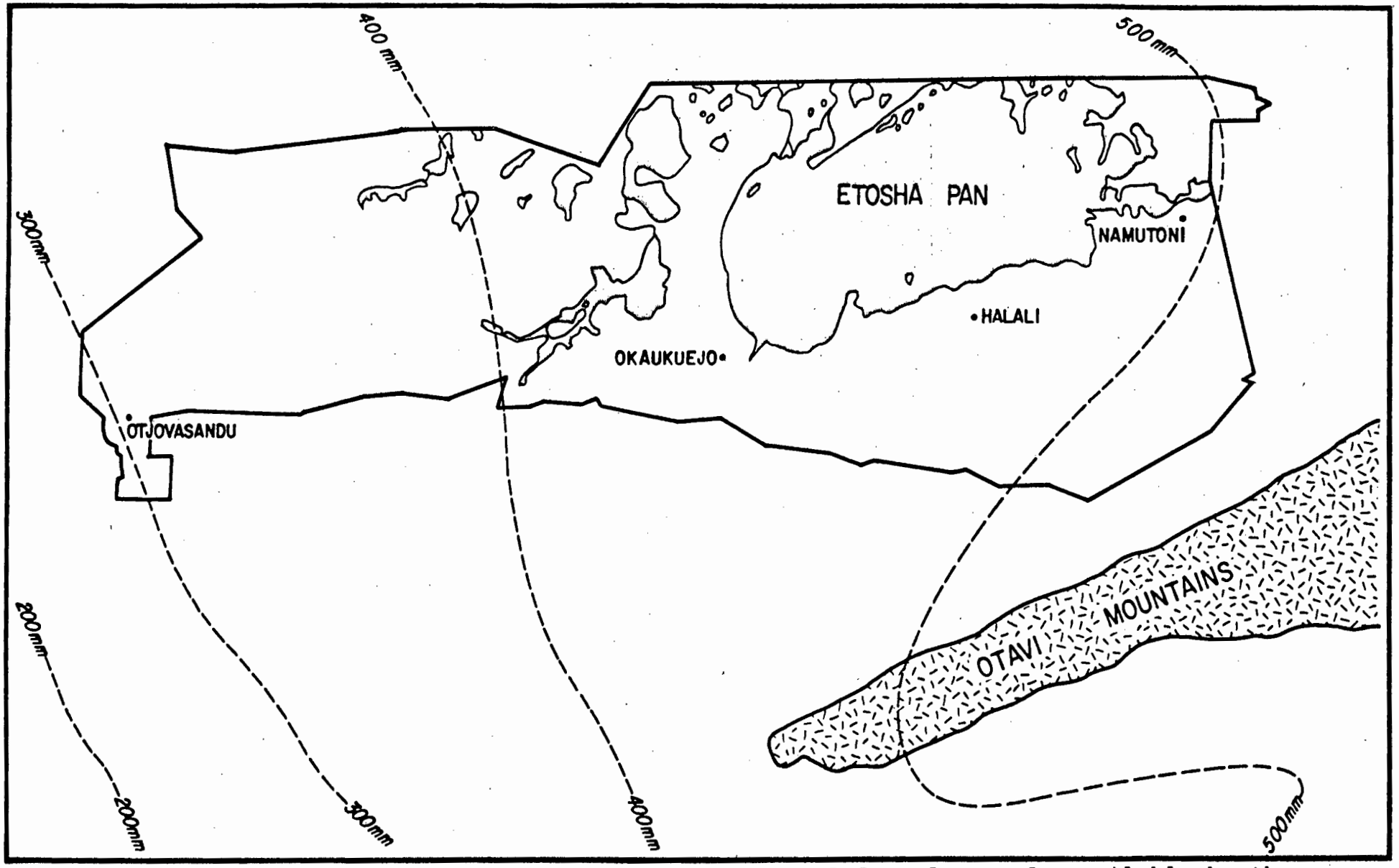

Fig. 2.4 : Isohyetal map of Etosha National Park, compiled from data made available by the Department of Transport, Weather Office, Windhoek.

2.2.4.1 Precipitation and Evaporation

Rainfall is the only measurable form of precipitation at Etosha. Dew, including white frost, precipitates in immeasurable amounts (< 0,1 mm) for up to four weeks after cessation of the rainy season. Nevertheless, dew may cause herbivores such as wildebeest to drink less frequently because it is available during their peak grazing period which is shortly after sunrise.

Nearly all of Etosha lies between the 300 - 500 mm isohyets (Fig. 2.4). It is of interest to note that the 500 mm isohyet appears to be extended eastward to form a bulge around the Etosha Pan. The latter, however, is not the cause of this deflection and it is the intrusion of the Otavi mountain range to the south of Etosha which is responsible for this effect (Weather Office records, Windhoek). Rain has been recorded at Etosha in all 12 calendar months, although in the 56 years during which measurements have been made (Table 2.1), there was measurable precipitation on only one day in July during this entire period (0,1 mm).

Although there is a continual increase in the average monthly rainfall measured at Okaukuejo, Halali and Namutoni from August onwards (Fig. 2.5), the amounts falling are too

Table 2.1 : Mean monthly rainfall recorded during 56 years at Okaukuejo (period 1901-78)

Measurement	Month											
	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
Mean Rainfall (mm)	0	0,2	1,7	8,4	31,1	73,3	92,7	107,7	75,1	26,0	1,6	0,5
Mean number of rain days	0	0,1	0,2	1,8	4,0	6,9	8,8	8,8	7,3	3,1	0,5	0,1
Mean number of rain days annually	41,6											

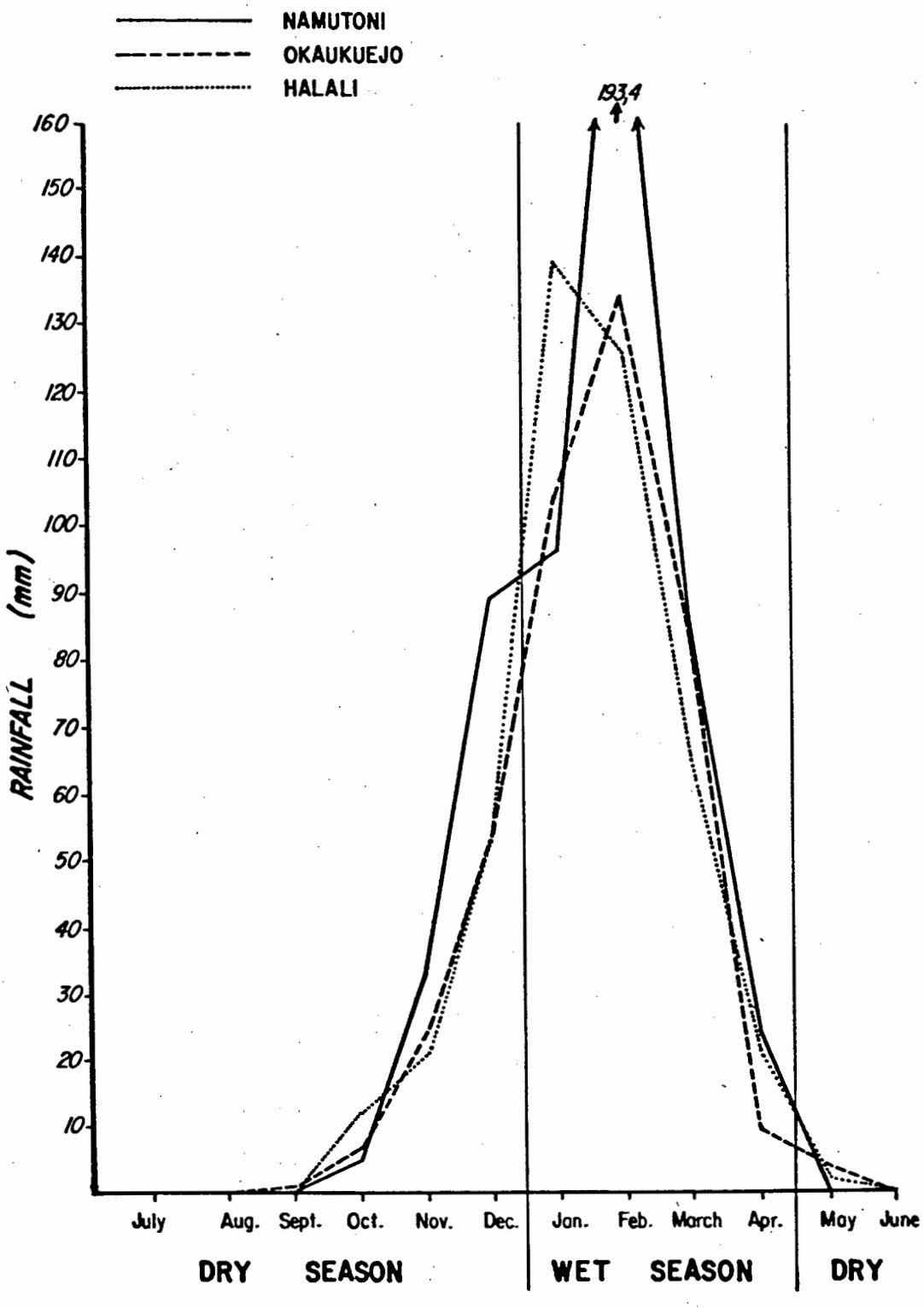

Fig. 2.5 : Mean monthly rainfall measured at Okaukuejo, Halali and Namutoni during the period 1974-78. The vertical lines demarcating the wet season are not superimposed directly over the rainfall period because the precipitation before January is usually insufficient to provide fresh grazing.

localised and insufficient to have any noticeable, direct effect on the migratory movements of wildebeest.

Only in January is the precipitation sufficient to cause significant sprouting in annual grasses and consequently the large scale migration of herbivores. February is the month with the most rain (25,7 % of Okaukuejo's annual total and 23,4 % of Namutoni's annual total), followed by January and March. The effective rainy season ends in April when maximum and minimum temperatures decline (Section 2.2.4.3). Table 2.2 shows the number of days during which measurable rain was recorded at Okaukuejo during the study period. Based on an arbitrary amount of 5 mm and more rainfall, Table 2.3 gives the number of days during which significant amounts of rain fell at Okaukuejo during this period.

Precipitation at Etosha is typically tropical with *Cumulus* and *Cumulonimbus* clouds developing, the latter becoming cirriform in the shape of an anvil. The resultant thunderstorms are usually moderate to heavy. On one such occasion (4 December 1934) a total of 106,2 mm of rain was recorded in 24 hours at Okaukuejo. Rainfall at Etosha can be localised and result in visible patchiness of grass cover. For instance, on 26 March 1978, Okaukuejo recorded 22 mm of rain while at Andersson Gate, a distance of 17 km

Table 2.2 : Number of days per month during which measurable rain (> 0,1 mm) occurred at Okaukuejo (1974 - 78)

Season	Month											
	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
1974/5	0	0	1	6	6	10	15	8	7	5	0	0
1975/6	0	0	0	1	7	4	20	14	12	4	0	1
1976/7	0	0	0	1	2	2	8	13	6	4	3	0
1977/8	0	0	0	0	1	14	11	16	6	1	0	0
Mean	0	0	0	2	4	8	14	13	8	4	1	1

Table 2.3 : Number of days per month during which more than 5 mm of rain occurred at Okaukuejo (1974 - 78)

Season	Month											
	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
1974/5	0	0	0	1	4	6	8	3	4	2	0	0
1975/6	0	0	0	0	2	3	11	5	10	2	0	0
1976/7	0	0	0	1	1	1	3	7	4	0	1	0
1977/8	0	0	0	0	0	5	8	12	2	1	0	0
Mean	0	0	0	1	2	4	8	7	5	1	0	0

south, only 3 mm was recorded. Annual rainfall is also erratic. Fig. 2.6 shows the fluctuations in yearly rainfall recorded at Okaukuejo since 1901.

Evaporation at Okaukuejo was measured daily during the study period, using a standard Class A evaporation tank (diameter 1,2 m, depth 25 cm). Factors affecting the rate of evaporation are humidity of the air, wind and radiation. The rate of evaporation, compared against rainfall is given on a monthly basis in Table 2.4. The average seasonal rate of evaporation measured at Okaukuejo (1974 - 78) was 2 662 mm, which exceeds the average seasonal rainfall of 436,8 mm during this period by a factor of 6,1. During these four seasonal years the monthly rainfall equalled the monthly evaporation once (January 1976) and exceeded it twice (February and March 1976).

2.2.4.2 Relative Humidity

The relative humidity at 08h00, 14h00 and 20h00, calculated from screened wet and dry bulb thermometers and measured at Okaukuejo during the study period is given on a monthly basis in Table 2.5.

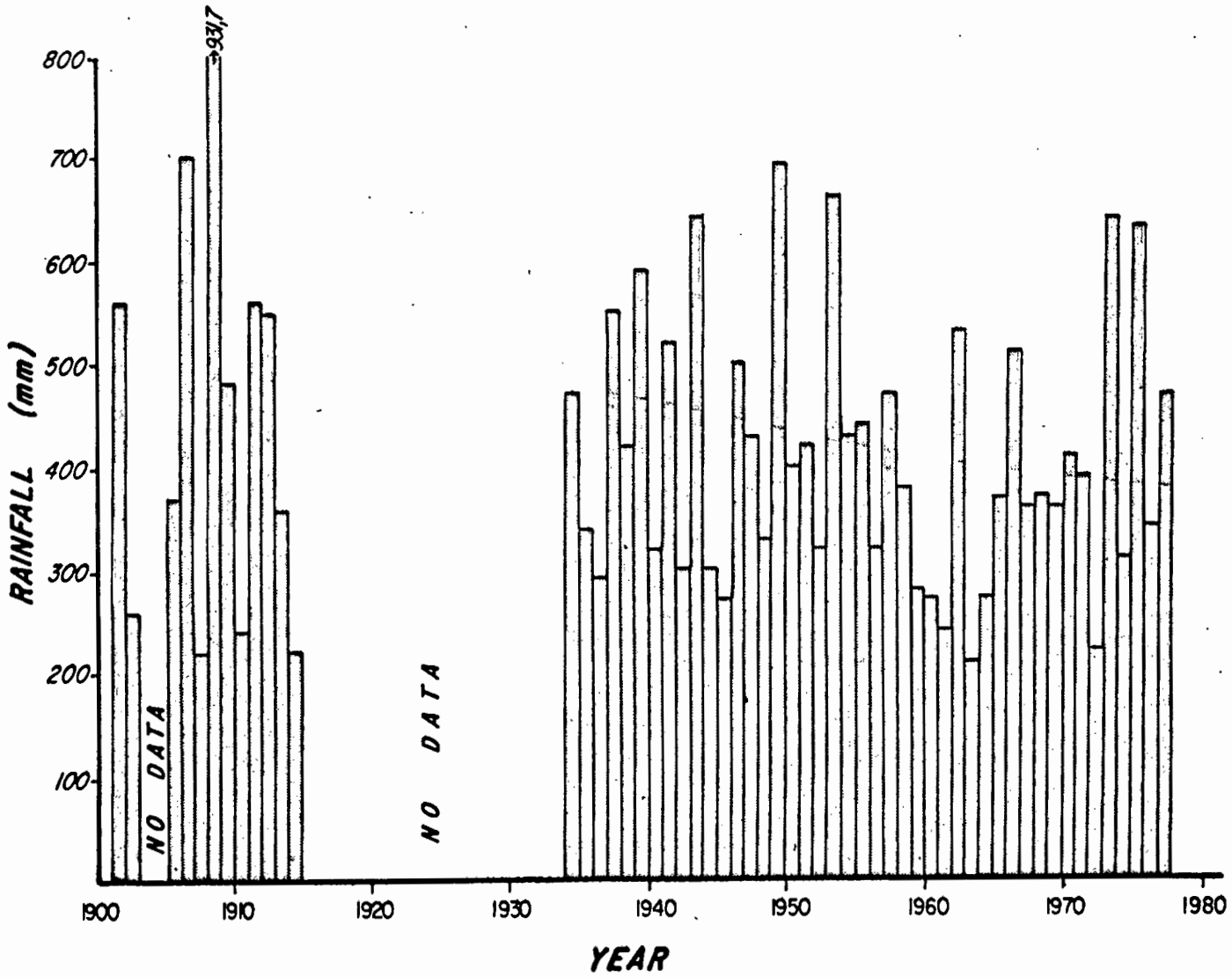

Fig. 2.6 : Yearly rainfall, measured on a seasonal basis, at Okaukuejo (1901-1978). The seasonal rainfall year extends from 1 July to 30 June.

Table 2.4 : Ratio of evaporation : rainfall at Okaukuejo (1974-78)

Season	Measurement	Month											
		July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
1974/5	Evaporation (mm)	216,9	243,3	309,4	295,2	280,6	330,1	296,0	269,7	211,6	185,3	215,9	201,2
	Rainfall (mm)	0	0	1,0	20,1	51,4	42,0	89,3	41,1	64,4	33,4	4,1	0
	Ratio	∞	∞	309,4	14,7	5,5	7,9	3,3	6,6	3,3	5,6	52,7	∞
1975/6	Evaporation	193,6	182,4	215,4	337,7	247,8	306,3	172,2	155,2	125,1	160,7	158,0	133,3
	Rainfall	0	0	0	1,4	30,4	42,7	171,7	169,9	211,5	50,0	0	0,2
	Ratio	∞	∞	∞	241,2	8,2	7,2	1,0	0,9	0,6	3,2	∞	666,5
1976/7	Evaporation	139,7	185,9	241,8	291,3	285,7	313,8	270,9	149,1	196,0	173,7	167,1	160,0
	Rainfall	0	0	0	6,3	10,4	12,6	43,8	104,9	44,1	14,7	13,2	0
	Ratio	∞	∞	∞	46,2	27,5	24,9	6,2	1,4	4,4	11,8	12,7	∞
1977/8	Evaporation	174,2	222,0	264,7	253,9	376,5	311,0	247,6	133,7	197,1	200,3	201,7	191,0
	Rainfall	0	0	0,5	1,4	1,6	111,9	108,9	221,6	10,6	15,2	0	0
	Ratio	∞	∞	529,4	252,8	235,3	2,8	2,3	0,6	18,6	131,6	∞	∞
Means	Evaporation	181,1	147,6	257,8	319,5	297,7	315,3	246,7	176,9	182,5	180,0	185,7	171,4
	Rainfall	0	0	0,4	7,3	23,5	52,3	103,4	134,4	82,7	28,3	4,3	0,2
	Ratio	∞	∞	644,5	43,8	12,7	6,0	2,4	1,3	2,2	6,4	43,2	857,0

Table 2.5 : Relative humidity recorded at Okaukuejo during the period 1974 - 78

Time of day	Measurement	Month											
		July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
08h00	Absolute maximum	91	80	81	96	95	92	96	97	99	99	93	92
	Absolute minimum	28	27	19	16	15	21	25	42	44	55	46	34
	Mean	55	44	42	41	48	49	68	80	84	80	68	59
14h00	Absolute maximum	37	50	71	80	84	85	96	98	92	87	51	41
	Absolute minimum	8	7	7	6	11	8	11	10	14	19	16	8
	Mean	22	18	16	20	24	25	41	49	48	42	28	25
20h00	Absolute maximum	59	47	65	61	89	93	95	99	93	90	91	95
	Absolute minimum	22	9	7	8	10	8	13	22	24	33	22	19
	Mean	36	29	25	26	32	33	55	64	65	57	44	43

2.2.4.3 Temperature

Screen temperatures measured at Okaukuejo during the study period and the number of days when screen temperature exceeded 25 ^{o}C, 30 ^{o}C and 35 ^{o}C are given on a monthly basis in Table 2.6.

2.2.4.4 Wind

Wind regimes measured at 08h00, 14h00 and 20h00 at Okaukuejo during the study period are given in Table 2.7 and Fig. 2.7.

2.2.4.5 Photoperiod

The annual photoperiod cycle at the latitude of Okaukuejo (19^{o}11'S, 15^{o}55'E) is illustrated in Fig. 2.8. The period between sunrise and sunset on 21 June 1977 was 10 hours 59 minutes (sunrise 07h26, sunset 18h25 S.A.S.T.) and on 22 December 1977 it was 13 hours 14 minutes (sunrise 06h16, sunset 19h30 S.A.S.T.). The difference in sun period between midwinter and midsummer is therefore 2 hours 15 minutes.

Table 2.6 : Screen temperature (^{o}C) at Okaukuejo during the period 1974 - 78

Measurement	Month											
	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
Absolute maximum	28,9	33,5	36,0	39,1	39,6	39,5	38,3	36,1	33,5	32,3	31,8	28,8
Mean maximum	25,6	28,2	32,4	34,2	34,5	34,8	31,9	30,3	29,8	29,3	27,3	25,2
Absolute minimum	1,5	-0,9	5,9	8,9	7,5	8,8	11,8	13,1	10,5	7,1	2,5	0,5
Mean minimum	6,1	8,3	12,6	16,5	17,8	17,4	18,2	17,4	17,0	14,8	11,4	6,6
Mean number of days exceeding 25 ^{o}C	21	28	30	31	30	31	30	26	31	30	28	17
Mean number of days exceeding 30 ^{o}C	0	9	26	30	28	31	21	15	15	16	2	0
Mean number of days exceeding 35 ^{o}C	0	0	3	11	14	16	6	1	0	0	0	0

Table 2.7 : Mean monthly wind regimes at Okaukuejo (1974 - 78)

Time of day	Measurement	Month											
		July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
08h00	Prevailing wind	SE	SW	SW	SW	SW	SW	SW	SW	SE	SE	SW	E
	Number of days of prevailing wind	3	4	4	7	6	8	5	7	8	3	3	2
	Absolute maximum force recorded (km/h) and wind direction	20	13	20	22	22	20	15	22	18	18	13	11
		NE	E	NE	SW	NE	SW	NE	SW	S	SE	E	SE
	Number of days when wind exceeded 20 km/h	0	0	0	1	1	0	0	1	0	0	0	0
14h00	Prevailing wind	NE	NE	NE	NE	N	NE	NE	NE	NE	NE	NE	NE
	Number of days of prevailing wind	23	15	12	11	7	9	12	14	9	17	18	19
	Absolute maximum force recorded and wind direction	46	38	36	31	36	27	30	31	29	31	32	27
		NE	NE	NE	NE	NE	E	NE	NE	NE	NE	NE	NE
	Number of days when wind exceeded 20 km/h	8	8	4	5	2	2	2	2	5	7	5	9

Table 2.7 (continued)

Time of day	Measurement	Month											
		July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
20h00	Prevailing wind	NE	SW	SW	SW	SW	SW	SW	SW	NE	NE	SW	SW
	Number of days of prevailing wind	4	2	5	8	9	10	6	7	4	3	1	1
	Absolute maximum force recorded (km/h) and wind direction	18 SW	18 SW	27 SW	37 SW	36 SE	38 NE	37 SE	25 E	31 NE	15 NE	7 SW	22 NE
	Number of days when wind exceeded 20 km/h	0	0	1	4	3	3	1	1	1	0	0	1

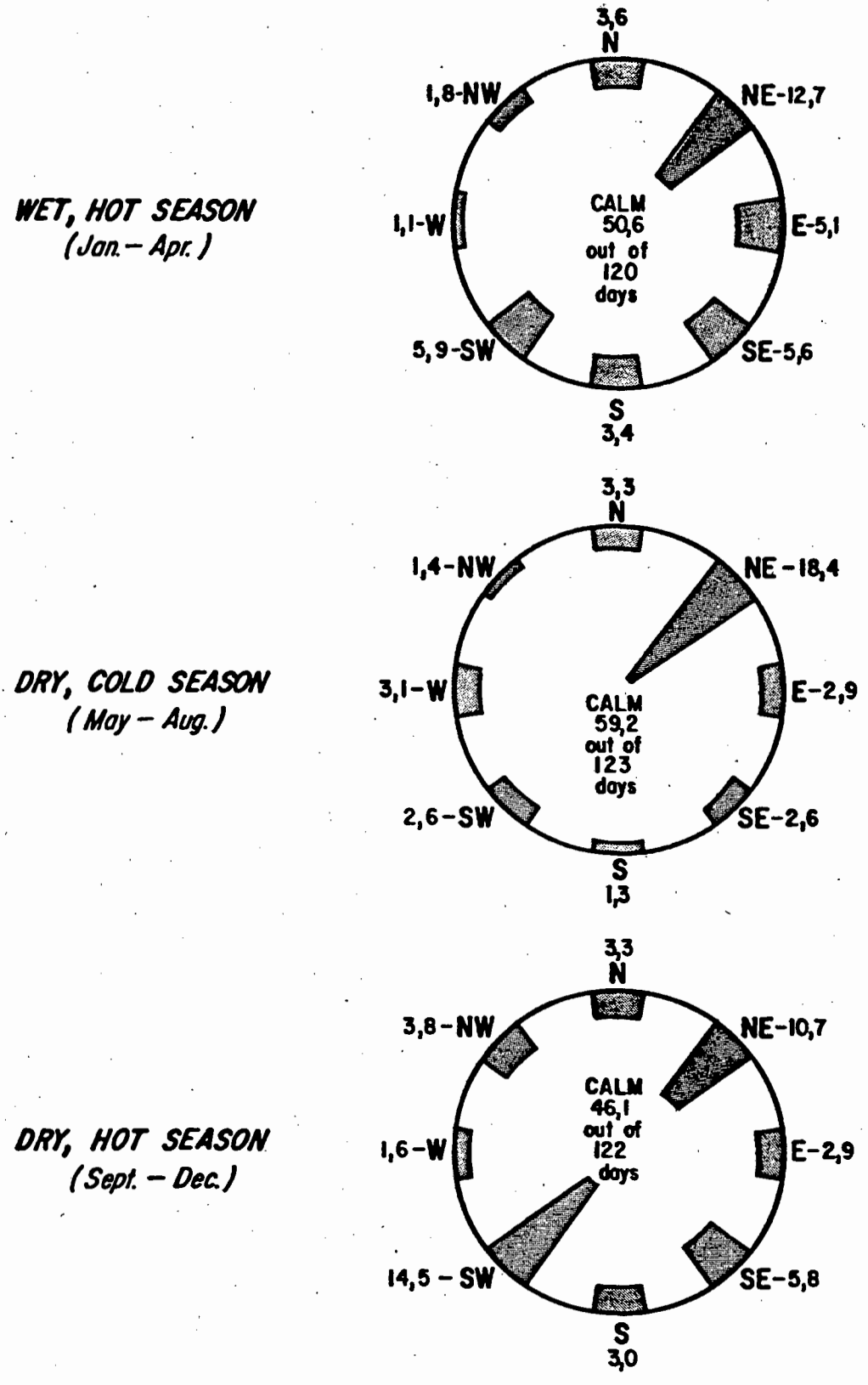

Fig. 2.7 : Wind regimes measured at Okaukuejo (1974-1978), showing the mean number of days of prevailing wind, on a seasonal basis.

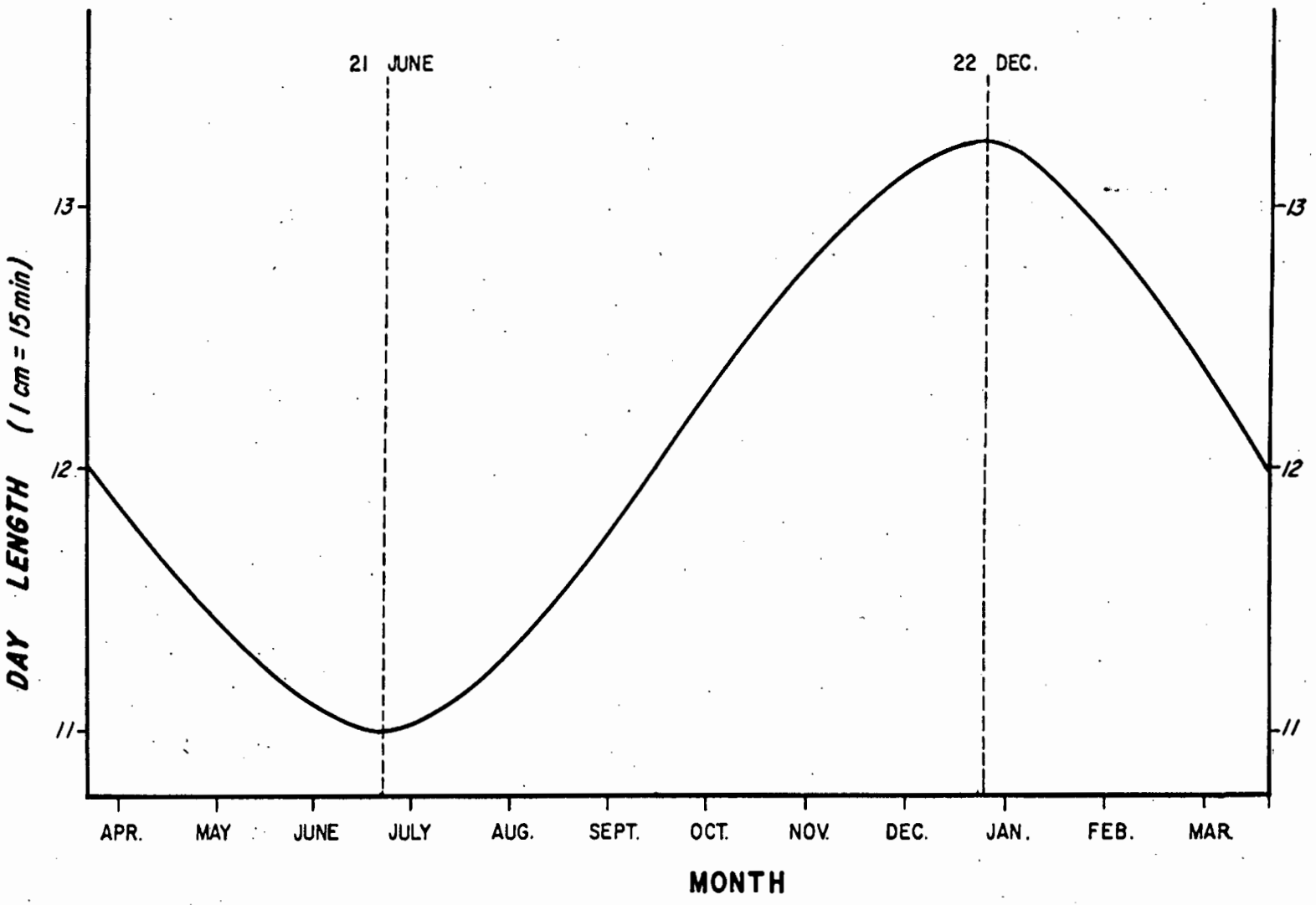

Fig. 2.8 : Annual photoperiodic cycle at the latitude of Okaukuejo (19°11'S, 15°55'E).

2.3 VEGETATION

In a preliminary map, Giess (1971) divided SWA into three main vegetation zones, namely : *deserts*, *savannas* and *woodlands*. Etosha occupies all of these zones, being further sub-divided according to Giess (1971) and illustrated in Fig. 2.9.

2.3.1 Main Vegetation Zones

2.3.1.1 Desert

The Etosha Pan and its immediate surroundings are unique to SWA and are termed "*Saline Desert with Dwarf Shrub Savanna Fringe*" (Giess, 1971). He describes this as a "quite barren" pan, fringed by halophytic vegetation which in turn adjoins the dwarf shrub savanna. However, although largely devoid of permanent vegetation, the Etosha Pan can, following good rains, produce tens of thousands of hectares of perennial grass *Sporobolus tenellus*. Pure stands of this grass develop especially in the south-western and north-eastern sectors of the Etosha Pan. Hence, as will be shown in subsequent discussion (Sections 7.3.7 and 8.4.2), the Pan may become an important source of food to wildebeest during the dry season.

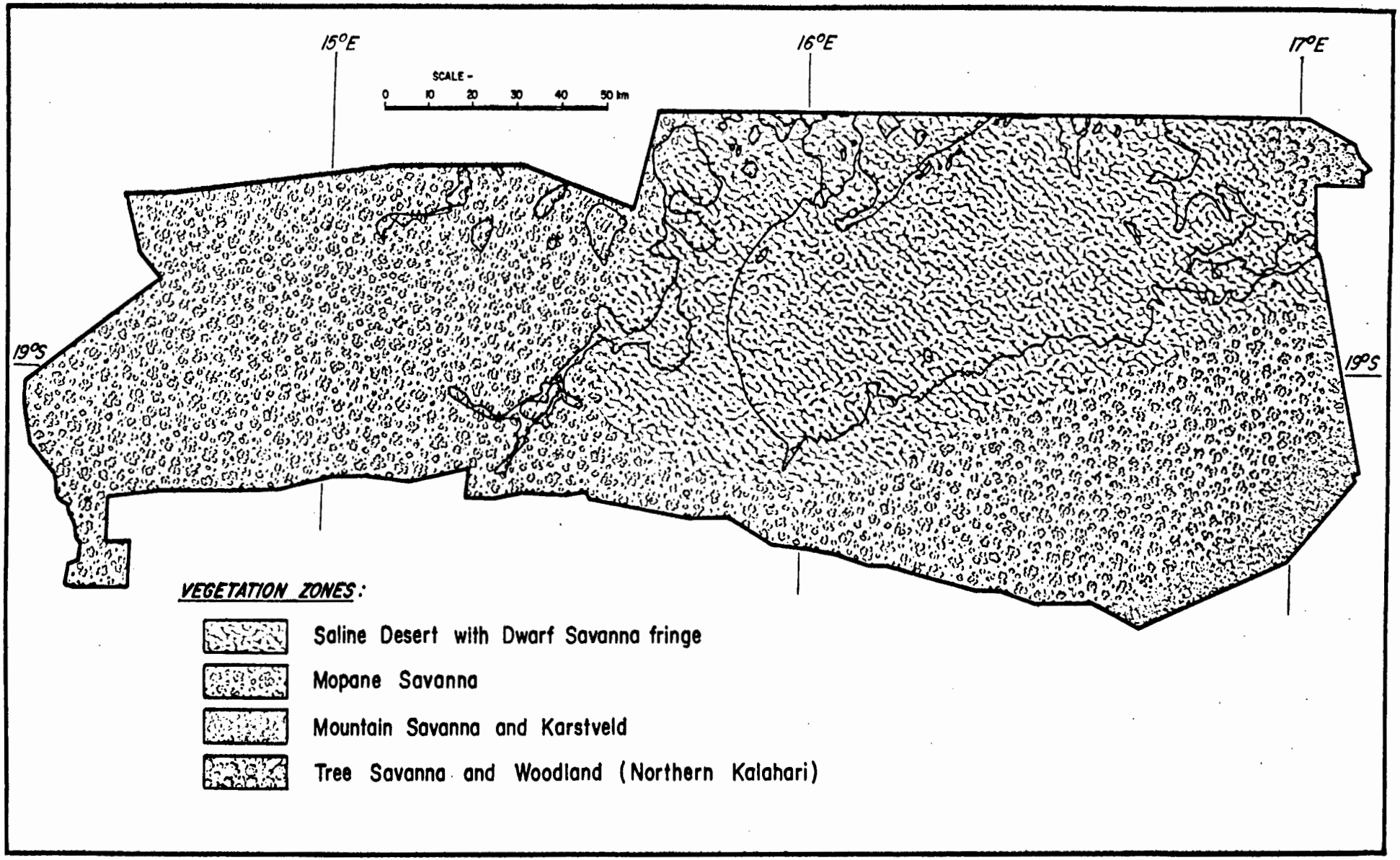

Fig. 2.9 : Major vegetation zones of Etosha National Park, according to Giess (1971).

Fringing the Pan on low terraces and in finger-like extensions of its main body, other halophytic grasses *Sp. spicatus* and *Odyssea paucinervis* flourish. Here, too, the shrub halophyte *Suaeda articulata* is prominent. Extending farther from the Pan the vegetation consists of *Salsola tuberculata*, *Leucosphaera bainesii*, *Petalidium engleranum*, *Cyathula* and *Monechma* spp. *Eragrostis* grass species are prominent in the rainy season. Adjacent to this lie thorn thickets which harbour mainly *Catophractes alexandri*, *Dichrostachys cinerea*, *Acacia nebrownii*, *A. mellifera* and *A. reficiens*. The desert zone is the major habitat of wildebeest at Etosha and I have accordingly listed the grasses recorded from this zone in Appendix 1.

2.3.1.2 Savanna

Mopane Savanna

This zone is dominated by *Colophospermum mopane* shrubs or trees and incorporates the major pedological regions such as the Kalkveld and Owamboland Sandveld (Fig. 2.3). Other tree genera which are well-represented are *Terminalia*, *Combretum*, *Albizia*, *Commiphora* and *Acacia* spp. The grass cover is largely perennial with *Triraphis ramosissima*, *Antephora pubescens*, *Monelytrum luederitzianum* and *Stipagrostis* spp. the dominant forms. A small percentage of the

wildebeest population (less than 5 %) occurs in the Mopane Savanna zone. Appendix 1 lists the grass species which occur.

Mountain Savanna and Karstveld

There is a close link between this vegetation and Mopane Savanna, with many plant species common to both. It occurs only in the extreme south-eastern corner of Etosha, namely the Central Highlands Dissected Region (Fig. 2.3). Typical tree forms found in it are *Moringa ovalifolia*, *Spirostachys africana*, *Combretum imberbe*, *Ficus* and *Acacia* spp. The grasses are similar to those of the Mopane Savanna (refer Appendix 1), but wildebeest have not been recorded in this part of Etosha.

2.3.1.3 Woodlands : Tree Savanna and Woodland (Northern Kalahari)

This zone is confined to the north-eastern corner of Etosha, occupying much of the Northern Kalahari Sandveld Region (Fig. 2.3). It comprises fairly dense stands of trees such as *Terminalia prunioides*, *Lonchocarpus nelsii*, *Ziziphus mucronata*, *Commiphora* and *Acacia* spp. Shrubs, especially *Croton* and *Grewia* spp. are common. Grasses occurring are *Antephora*, *Aristida*, *Digitaria*, *Enneapogon*,

Urochloa and *Schmidtia* spp. (refer also to Appendix 1). Wildebeest occur here in small numbers, notably on the isolated Beiseb Pan (Fig. 2.3).

2.3.2 Detailed Vegetation Types

The first detailed vegetation map of Etosha is available from Le Roux (1973). I have simplified Le Roux's classification of vegetation types in Fig. 2.10, indicating in the key which types are inhabited by wildebeest. In all, eight of the 21 vegetation types in Etosha appear to be suitable wildebeest habitat for at least part of the year.

2.4 MAMMALS

For the purpose of this study, I classified "larger" and "smaller" mammals according to Dorst and Dandelot (1970).

2.4.1 Larger Mammals

A total of 55 species of larger mammals have been recorded at Etosha. They represent 11 Orders and 22 Families. The Bovidae are the best represented with four Sub-families and seven Tribes. A complete species list is given in

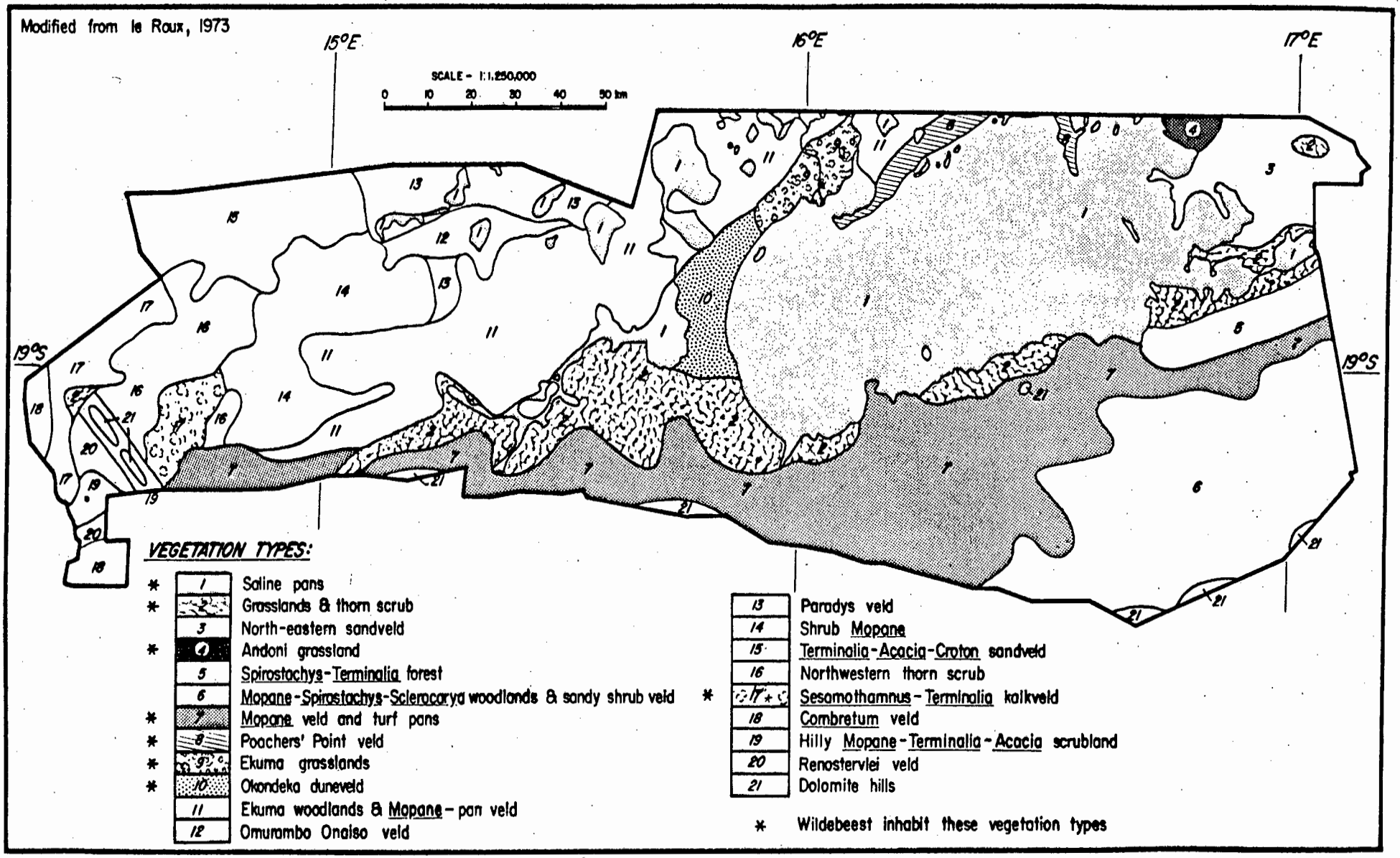

Fig. 2.10 : Detailed vegetation types of Etosha National Park, simplified from Le Roux (1973).

Appendix 2 and, where known, the approximate number of each species. Species of mammal referred to in the text, which do not occur at Etosha, are listed in Appendix 3. I will subsequently use only the common names of species in the text.

2.4.2 Smaller Mammals

Thirty-eight species of smaller mammals are known to occur at Etosha and it is likely that more will be recorded. Three Orders and 11 Families are represented. The Rodentia are probably the most numerous (Dixon, 1979, Dept. report).

2.5 MANAGEMENT AND TOURISM

Etosha has, for the sake of management, been divided into four areas, each of which has a permanent base from which conservation staff operate. From east to west (Fig. 2.1) these are : Namutoni (3 800 km^2), Halali (4 363 km^2), Okaukuejo (9 607 km^2) and Otjovasandu (4 500 km^2).

The Namutoni area is sub-divided into two (Fig. 2.1). Similarly, Okaukuejo has three sub-divisions and Otjovasandu has two sub-divisions. Halali is undivided. Thus Etosha has eight sub-divisions, each of which is patrolled by a

Nature Conservator. At Namutoni, a Senior Nature Conservator is stationed, and co-ordinates the work of the Namutoni-Halali areas. Similarly, two Senior Nature Conservators co-ordinate work in the Okaukuejo-Otjovasandu areas. The combined activities of all the conservators in Etosha are the responsibility of a Principal Nature Conservator, stationed at Okaukuejo.

Being centrally situated, Okaukuejo is the headquarters for Etosha's management staff. In addition to the conservation staff, the research section is located there, at the Etosha Ecological Institute. Two full-time professional officers are employed in research : a biologist and a veterinarian. They are assisted by a Senior Nature Conservator and a Nature Conservator who serve as technical assistants and are not directly associated with the other Etosha conservators. The research section is complemented from time to time by seconded officers from the SWA Division of Nature Conservation and Tourism as well as by visiting scientists.

Tourism plays an important role in Etosha and facilities for tourists exist at Namutoni, Halali and Okaukuejo. The Otjovasandu area is not yet accessible to tourists. In 1977 a total of 45 927 tourists visited Etosha, of which 8 026 came from overseas, 20 402 from the Republic of South

Africa and 17 499 from SWA. They travelled in a total of 9 838 vehicles and brought a gross revenue of R956 681 to Etosha. This is 43 % of the total tourist revenue of R2 208 153 for SWA in 1977 (Annual Report of the Division of Nature Conservation and Tourism, Windhoek, 1977).

2.6 HISTORICAL REVIEW OF CONSERVATION AND RESEARCH AT ETOSHA

2.6.1 Early European Visitors and Their Influence

The earliest written account of the area surrounding the Etosha Pan in SWA which could be traced, is given by Andersson (1856). He arrived at the edge of the Pan, in the company of another explorer, Galton, on 29 May 1851. In his narration he describes the impression of lushness he obtained from the reeded and "most copious fountain", which he refers to as an Owambo cattle post, and which is probably the site of the present-day Namutoni rest camp in the Etosha National Park. Andersson (1856) observed herds of 3 000 - 4 000 cattle as well as zebra and springbok in the area surrounding the fountain. Andersson's route to Owamboland (Owambo), lying east of the Etosha Pan, was the first to be opened to trading and was followed by trade routes to the west of the Pan. McKiernan (in Serton, 1954)

travelled northwards via Okoquea (presently the main tourist rest camp of Okaukuejo) on 2 August 1876. He gave a graphic description of the abundance and variety of wild animals, stating that

> "all the menageries in the world turned loose would not compare to the sight I saw that day".

Further to the north McKiernan entered a vast plains area, which is probably the southern "pan veld" of Owambo, where he encountered wild animals in such abundance that he was moved to say :

> ". . . we fell in with immense numbers of animals beyond anything I had yet seen. I would scarcely be believed, if I should state that there were thousands of them to be seen at a sight. Gnus in herds like the buffalo on the plains /viz. of North America/, hundreds of zebras, ... springboks by tens of thousands, ostriches, gemsboks, steinboks, hartebeeste and elands. Water and grass were plentiful and they seemed to be having an easy time of it . . . ."

The early trader routes to the east and west of the Etosha Pan were followed by the Dorstland (Thirstland) Trekkers who passed through the area between 1876 and 1879

(Trümpelmann, 1948). The majority passed on to Angola but a few families returned in 1885 with the intention to farm south of the Etosha Pan. They named the area Upingtonia, but the settlement was short-lived and became abandoned in 1887 following clashes with the neighbouring Owambos and Hereros as well as local Bushmen. German troops were stationed at Namutoni and Okaukuejo in 1896. They were under orders to shoot the wild animals to aid in curbing the spread of rinderpest virus to cattle (Fischer, 1914).

The first fort was built on slightly elevated ground near the Namutoni fountain in 1899 by the German cavalry who recognised the tactical advantage of controlling this area (Fischer, 1914). Later, in 1904, the fort was burnt and totally destroyed by marauding Owambos. It was rebuilt in 1905 as a police outpost and the shooting of wild animals by the authorities, who used machine guns, continued (Fischer, 1914). The fort later fell into disuse and became derelict until its restoration in 1956 as a tourist attraction and accommodation. Similarly, at Okaukuejo, the control of rinderpest virus gave rise to a police outpost in 1909 and ultimately to a tourist rest camp in 1952 when development of Etosha for large-scale tourism commenced.

2.6.2 Definition of Boundaries

The proclamation of Etosha as a "game reserve" was made by the Governor of German South West Africa, Dr. F. von Lindequist on 22 March 1907 (Ordinance 88 of 1907), when the area was named "Wildschutzgebiet Nr. 2", covering an area of 99 526 km^2 (Fig. 2.11). After 1958, "Game Reserve No. 2" became known as the "Etosha Game Park" or the Etosha National Park. The popular name of "Etosha Pan" is misleading and should be applied only to the main saline pan depression in Etosha National Park. Ordinance 88 (1907) made provision for farmland still under private ownership within Etosha's boundaries and for trading rights on that land. Private land ownership lapsed in 1935 with the exception of one small erf near Okaukuejo which is legally still private property (Lenssen, 1977, pers.comm.). In drought conditions emergency grazing rights for farm livestock were also granted (Executive Committee of SWA, Minute 334 of 1962) when an 8 - 16 km strip inside Etosha's southern boundary was declared open to farmers. De la Bat (1962, Dept. report) estimated that 110 000 head of livestock grazed in this corridor. Since its proclamation, Etosha has undergone many minor and several major boundary alterations, *vide* Proclamation 26 (1928), Government Notice 374 (1947), Ordinance 18 (1958), Government Notice 117 (1967), Ordinance 21 (1970). For the effect of the major

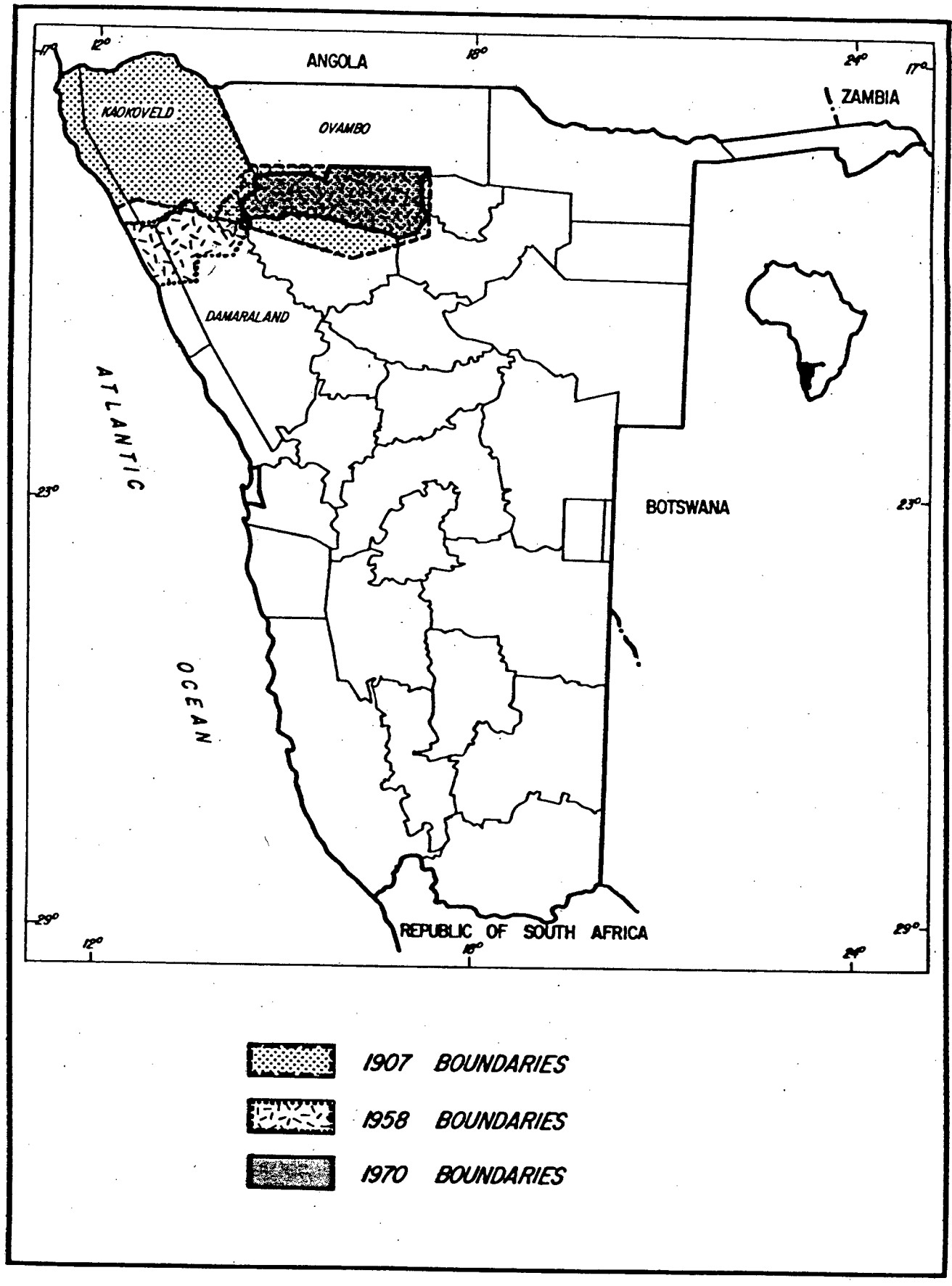

Fig. 2.11 : Changes made to the boundaries of Etosha National Park between 1907 and 1970.

boundary alterations on the original area of Etosha refer to Fig. 2.11.

Initially, the definition of Etosha's boundaries made virtually no impact on the movement of wild animals, except for the legal technicality that after crossing a mapped line, they were not protected. Physically the boundaries consisted of surveyed points and later fire-breaks were cleared along some of them. Migratory herds were therefore unrestrained in their movement along traditional routes. The first fences to be erected by European farmers on the southern boundary of Etosha during the period 1955 - 60 were of minor consequence because they were discontinuous and easily broken (Van Wyk, 1978, pers.comm.). However, an epidemic of foot-and-mouth disease in the northern areas of SWA during 1961 resulted in the erection of a "game-proof" fence as a veterinary measure along the eastern and southern boundaries of Etosha (Fig. 2.1). It is 2,6 m in height with 17 strands of wire and reinforced by a 1,5 m wire mesh which is embedded into the ground. The complete fencing of Etosha's boundaries, as defined by Ordinance 21 (1970), was accomplished in 1973 with the erection of the western and northern boundaries' fences which border the tribal areas of Damaraland, Kaokoland and Owambo. The fence has a total length of 1 640 km, all of it "game-proof", except

for 325 km from Omutamba Maowe to the Ekuma River (Fig. 2.1) which is 1,3 m in height with 9 strands. The area thus enclosed is 22 270 km^2. Fencing of Etosha curbed the majority of animal movement except for elephant which easily break or trample the relatively flimsy structure and warthog which often burrow underneath it. Destruction of the fence by elephants was severe at points where it bisected their traditional migration routes to the west, north and north-east as well as along the southern boundary where they crossed to drink from water points for domestic stock. Subsequently, elephant-proof fencing was erected along the most sensitive areas (Fig. 2.1). The elephant-proof fence, constructed two metres from the "game-proof" fence on the Etosha side, has 3,2 m double railway-lines which have been welded together and sunk 1,1 m into cement. They are spaced 180 m apart. Between them single and double railway-line poles are erected alternately every 7,5 m. In addition, four hanging wooden poles, 100 mm in diameter and 2 m in length, are added to the 7,5 m spaces. Four steel cables of 13 mm diameter are strung horizontally through the railway-line poles and spaced 50 cm apart.

Approximately 90 km of elephant-proof fence have been constructed, with a further 40 km scheduled for erection in 1980. Cost of materials and construction is about R12 000 per kilometre (SWA Tender Board Contract No. 1822/77).

2.6.3 The Faunal Status of Etosha up to 1952

Fischer (1914) described the migration of wild animals in the precincts of Etosha, being the first person to publish on this phenomenon, but he did not quantify his observations. The earliest census of large animals in SWA was undertaken in 1926 (Section 1.1.2.2).

Because the fauna of Etosha and Owambo was indivisibly integrated at that time, it is necessary to regard the data supplied as valid for Etosha. Furthermore, the Game Warden was stationed at Namutoni and patrolled the eastern part of "Game Reserve No. 2" more extensively. His census figures were obtained in the area delineated in Fig. 1.2. Table 2.8 gives the results of the 1926 census and is set out in decreasing order of numerical importance. The census was limited to ground counts of animals and large areas of Etosha were inaccessible. The resultant approximation of numbers of the more conspicuous species should be taken as the minimum. In the case of nocturnal and secretive species such as leopard, cheetah, hyaena, steenbok and Grimm's duiker, the relatively high numbers given must be treated with caution as they could be little more than enlightened guesses. Similarly, the figure of 2 200 for wild dog is extraordinarily high. The data reflected in Table 2.8 are supported by information given

Table 2.8 : Ground census of selected species in the Etosha Pan - Owamboland regions during 1926, based on data contained in reports to the Secretary for South West Africa (File A.201/10)

Species	Species		Total
	Etosha Pan	Owamboland	
Burchell's zebra	20 000	1 200	21 200
Springbok	16 000	5 000	21 000
Wildebeest	15 000	2 500	17 500
Steenbok	11 000	5 000	16 000
Grimm's duiker	7 000	3 000	10 000
Kudu	7 000	350	7 350
Gemsbok	6 000	1 200	7 200
Ostrich	6 000	600	6 600
Hyaena, brown & spotted	4 000	300	4 300
Kori bustard	3 000	600	3 600
Wild dog	2 000	200	2 200
Red hartebeest	1 500	600	2 100
Eland	600	500	1 100
Leopard	1 000	-	1 000
Cheetah	900	80	980
Warthog	300	250	550
Black-faced impala	0	400	400
Roan antelope	0	250	250
Hartmann's zebra	150	100	250
Lynx and Serval	-	250	250
Lion	200	10	210
Bush pig	100	100	200
Klipspringer	30	150	180
Damara dik-dik	150	15	165
Giraffe	60	40-50	100-110
Oribi	30	40-50	70- 80
Elephant	0	40-50	40- 50
Buffalo	0	5	5
Southern reedbuck	0	5	5
Black rhinocerus	0	2	2
Hippopotamus	0	2	2

in Jaeger (1926-7) who said that in 1913 between 20 000 and 30 000 animals could be seen on the plains of Etosha and estimated that more than half were wildebeest.

Although Shortridge (1926-7, 1934) drew attention to seasonal movement of animals around the Etosha Pan, no quantitative data of Etosha's fauna could be traced for the period 1927 - 52. The State Library archives in Windhoek confirm that very few relevant records exist for Etosha during this time. The appointment of the first professional biologist to Etosha was made in 1947. Estimates of animal numbers made by his successor in 1951, P. Schoeman, show considerable latitude. For instance, his estimates (Schoeman, 1952 Dept. report) are : Burchell's zebra (10 000 - 15 000), wildebeest (7 000 - 10 000), springbok (5 000 - 7 000), gemsbok (800 - 1 200). In 1951 Schoeman recommended that 1 000 Burchell's zebra and 500 wildebeest be culled to assist in rehabilitating the grasslands of Etosha which he considered to be severely overgrazed. Culling ceased a year later, the official records showing that 300 zebra and 120 wildebeest were taken. However, the opinion of conservationists in the Territory is that the figures are questionable and that several thousand animals were shot.

2.6.4 The Period 1953 to 1964

The first reliable information and collection of quantitative data were facilitated with the appointment of B. de la Bat as Chief Game Warden in 1954 and the creation of the Nature Conservation Section in 1955. Estimates of wildebeest numbers range from 25 000 (De la Bat, 1977, pers.comm.) to 30 000 (Viljoen, 1967, Dept. report). De la Bat (1960, Dept. report) mentions an aggregation of 18 000 wildebeest on the Andoni plains alone. During the same period Van der Spuy (1960, Dept. report) records that mass mortality of animals occurred on the southern plains of Owambo when drought conditions caused the death of 4 000 wildebeest in August 1959.

Prior to the restriction of wild animal movement brought about by the erection of "game-proof" fences between 1961 - 1973, Etosha supported very large, temporary influxes of migratory animals during the rainy season. For instance, De la Bat (1962, Dept. report) estimated that the antelope and other large herbivores numbered 100 000 individuals.

Visiting researchers contributed considerably to knowledge of Etosha during this period, notably Bigalke (1961), who published the first scientific account of the area's

general ecology. His observations, made during the period 1956 - 58, defined the "dry season concentration area" south of the Pan and the "wet season dispersal area" to the west of it. Bigalke (1961) did not consider the Namutoni - Andoni areas to fall in either of these zones and treated them separately. In his opinion, migratory game congregated at Namutoni during the dry season and remained there until the height of the rains. Andoni was regarded as an area of intermittent game concentration during the rainy season.

Although detailed road and waterhole counts of animals were provided by Bigalke (1961), the species' population totals during the 1953 - 64 period were sketchy and only approximations are available. For instance, Bigalke (1961) records an estimated 10 000 migrant Burchell's zebra, wildebeest and springbok west of Etosha Pan in February 1957. A light aircraft was seconded to Etosha in this time but regular, detailed aerial surveys were not possible (De la Bat, 1977, pers.comm.).

2.6.5 The Period 1965 to 1973

A permanent research section under the Director of Nature Conservation and Tourism was created in Etosha in 1965 when the first veterinarian and two ecologists were appointed. During the period 1965 to 1973 the most significant research

relating to wildebeest in Etosha was done by Ebedes (1976a, b) who found that the species was highly susceptible to anthrax (35 % of all anthrax-infected carcases found). Furthermore, Ebedes *et al.* (1977) successfully immobilised 13 wildebeest in Etosha with etorphine hydrochloride (M-99, Reckitt) in order to mark them. He subsequently established that two of these wildebeest moved a distance of at least 160 km from the point of capture. The only other publication during this period which is relevant to the present study was the discovery of a new species of dipteran larva *Oestrus dubitatus* which parasites the nasal cavities of wildebeest (Basson and Zumpt, 1969). Other than the aforementioned research, no detailed investigation into the ecology of wildebeest at Etosha has been carried out.

Section 3

GENERAL PROCEDURE

Here I will outline briefly the procedure adopted during each phase of the investigation. Detailed methods appear in subsequent sections and a summary of the results and conclusions is provided at the end of each section. Finally, in Section 13, I synthesize the implications of my findings and make recommendations for a management strategy to halt and possibly reverse the decline in wildebeest numbers at Etosha. Although several of the investigations were run concurrently between 1974 - 78, I treated each one separately when reporting the results. This allows a progressive approach to the problem and assists the sequence of arguments which I present in this thesis.

It should be mentioned that all my observations were made on free-ranging wildebeest, except when individuals were temporarily immobilised for marking and the collection of blood and faecal samples. Samples such as rumen contents, bone marrow, kidneys and urine were collected from wildebeest which were shot for veterinary investigation. It is necessary to stress that although fresh wildebeest carcases were regularly located in the field, they were mostly

anthrax-infected. Veterinary regulations precluded that any of the above samples could be obtained from them. The processing of skulls, found in the field, for age determination, was permissible only after total immersion of the material in 10 % formalin for 24 hours to destroy anthrax bacilli.

3.1 ACTIVITY PATTERNS

The purpose of determining these patterns in wildebeest was to quantify their activity cycle over a period of one year to provide baseline data which could be used to construct an energy budget for maintenance and activity. Consequently, I measured the 24-hour activity cycle of the major age, sex and social classes of wildebeest on a monthly basis, applying the "focal-animal" method on marked individuals, and the "instantaneous scan" method on unmarked herds. The activity data, together with recorded environmental conditions, were analysed by computer, using time intervals of 15 minutes which were subsequently sorted on an hourly, daily, monthly and seasonal basis.

3.2 ENERGY BUDGET

The measured activity of wildebeest was translated into an

energy demand by allocating theoretical energetic values to each of the various activities, using data from domestic ruminants. Thereby an estimate of the energetic cost of maintenance and activity in wildebeest was obtained. To complete the energy demand of free existence, the phenomena of growth, gestation, lactation and homeothermy were also considered and included in the energy budget by applying formulae, based on domestic ruminants, which incorporated the characteristics of Etosha's wildebeest. To estimate a yearly energy budget for the population, I took cognizance of the energy requirements in the various age-sex and social classes of wildebeest and their numerical contribution to the population. Because the amount of energy in the available grass did not fluctuate to any great extent during the year, and the fact that wildebeest exhibited a well balanced energy consumption, it was not considered necessary to calculate energy budgets on a seasonal basis.

3.3 PROTEIN BUDGET

As in the case of the energy budget, the purpose of constructing a protein budget for wildebeest was to estimate individual requirements for the basic life processes of maintenance, growth, gestation and lactation. Thus I calculated the endogenous urinary nitrogen, the metabolic

faecal nitrogen and the retained nitrogen, using basic formulae obtained from research on domestic ruminants, and incorporating in them the characteristics of Etosha's wildebeest. Thereafter, I converted the nitrogen requirement into a protein requirement by multiplying with a factor of 6,25 and subsequently calculated the population's protein budget on a seasonal basis. In doing this, I took into account the contribution made by the major age-sex-social classes in terms of their numbers. In contrast to the energy budget, it was desirable to know the seasonal protein requirement in wildebeest. This was because of the highly seasonal protein demand in pregnant and lactating cows and also the seasonality of protein content in the forage.

3.4 NUTRITION

I quantitatively determined whether sufficient food and water were available to wildebeest and what the quality was on a seasonal basis. To achieve this, an estimation of grass production and its removal by herbivores was obtained by measuring protected and unprotected (grazed) stands of grass. Grass samples were collected at the sprouting, seeding and dormant stages of their growth and analysed for crude protein, crude fibre, soluble carbohydrates, fat,

ash, water and gross energy. The gross energy available in grass was subsequently refined to metabolisable energy, using a standard formula. Faecal samples, collected on a seasonal basis, were also analysed for these components. In addition, I attempted an estimation of the seasonal food intake by the population and coupled this to a similar estimate of the faecal production, thereby obtaining a digestibility value for the forage. Rumen contents were evaluated by identifying the structural components of grass on a seasonal basis.

To determine water quality, detailed bacteriological and chemical analyses were undertaken on water sampled from man-made boreholes, artesian wells, natural fountains and a river. Rainwater from pools was only analysed for chemicals. I then related the observed drinking habits of wildebeest to their renal capabilities. Kidney efficiency was determined by relating medulla thickness to kidney size and the ability of wildebeest to reduce water loss via their urine was tested by measuring the blood plasma : urine osmotic ratio on a seasonal basis. In addition, wildebeest milk was analysed for its nutritive and energy levels.

3.5 NUTRITIONAL BALANCE

The energy and protein requirements of the major food competitors of wildebeest were similarly established, taking into account their age-sex ratios and population trends. Five species of large herbivores were considered for this purpose, namely, Burchell's zebra, springbok, gemsbok, red hartebeest and ostrich. Having thereby obtained total energy and protein requirements for the large herbivores, including wildebeest, I then balanced the measured supply of energy and protein by the grasslands against the combined theoretical demand to establish whether a seasonal or yearly shortfall of nutrients occurred between 1974 - 78. In addition, I examined the nutrient supply in relation to available drinking water to compare the relative food-water dependence of wildebeest with the other large herbivores.

3.6 NUTRITIONAL STATUS

To assess the nutritional status or "condition" of wildebeest on a seasonal basis, I judged their external physical appearance according to five categories of visual rating. I also measured the kidney fat, bone marrow fat and nine parameters in the blood plasma of wildebeest which were

shot at the height of the wet and dry seasons respectively. Furthermore, macro and trace elements were measured in the liver of shot wildebeest and gross microscopic scanning of peripheral blood smears was undertaken for possible anaemia and other haemocytic abnormalities.

3.7 DISEASE AND PARASITES

To establish the role of disease and parasitism in the decline of wildebeest at Etosha, a total of 25 animals, representing the major age-sex and social classes, were shot selectively at the height of the wet and dry seasons. Veterinary specialists were requested to sample and examine organs, tissues, blood, urine and the alimentary contents of these wildebeest. In addition, ectoparasites and dermal scrapings were collected on a seasonal basis from 60 immobilised wildebeest. To monitor the level of anthrax at Etosha, blood smears from all fresh carcases of wildebeest and other large herbivores were examined microscopically.

3.8 PREDATORS AND SCAVENGERS

The predator : prey biomass ratio was regarded as the most

practical assessment of whether predation at Etosha could be considered to be within acceptable limits. Consequently, the numbers of major predators inhabiting the grasslands, namely lion, spotted hyaena and cheetah, were estimated and their age-sex ratios and group size were determined from field observations. Also, the prey preferences of these predators were calculated from observed kills and an estimate of their mean daily food intake was made. These data enabled me to balance the annual food demand of predators against the live mass of available prey.

3.9 POPULATION STRUCTURE

In concluding the investigation, I wished to examine the population structure of wildebeest at Etosha, estimate its total size and establish the trend in numbers during the period 1974 - 78. Eight aerial censuses were undertaken, five of them by helicopter and three by fixed-wing aircraft. To check the accuracy of the aerial counts, I estimated the total population by Lincoln Index, using wildebeest which had been marked and subsequently released into the free-ranging population. To obtain age-sex ratios, observations were made on whole herds, mainly during ground counts, but also during aerial census when lone, territorial bulls and bachelor herds could be

identified. Mortality patterns of the population were established by tooth attrition in a sample of 283 skulls. Finally, I constructed a predictive model, based on critical parameters such as predation/mortality rate, calf survival rate and birthrate, to project future trends in the wildebeest population at Etosha.

Section 4

ACTIVITY PATTERNS

4.1 INTRODUCTION

The purpose of this study was to quantify the activities of free-ranging wildebeest at Etosha by apportioning their 24-hour activity cycles into mutually exclusive categories over a period of one year. The length of time spent in each activity could then be calculated as a percentage. These baseline data were subsequently used to construct an energy budget for maintenance and activity in wildebeest by allocating energy values to each of the various activities. In this manner I proposed to test whether the energy demand made by the wildebeest population was equalled by the energy produced in their forage. The resultant positive or negative energy balance would indicate the extent of habitat utilisation and permit conclusions to be made in regard to food energy supply as a limiting factor for the wildebeest at Etosha.

In addition, the data potentials provided by an activity study were considerable, allowing comparisons between the different age, sex and social classes of wildebeest. In

this way vulnerable components of the population with regard to energy requirements could be identified. The manner in which activity was recorded also provided information about habitat preferences, influence of climate and other animal species, as well as sequential states in time.

Literature about the activity patterns of free-ranging African ungulates is still very limited. For the present investigation I referred mainly to the information published by Jarman and Jarman (1973), Walther (1973), Leuthold (1977) and Sinclair (1974, 1977). I was unable to trace any published or unpublished work relating to the quantitative analysis of diurnal, nocturnal or seasonal patterns of activity in unrestrained wildebeest. The methods by which data were collected were based largely on those advocated by Altmann (1974), using procedures adapted from Davidge's (1975) study of wild baboons.

4.2 METHODS

4.2.1 Focal-animal Studies

The term "focal-animal" is taken from Altmann (1974) and refers to any sampling method which

(i) records all occurrences of specified actions (or interactions) of an individual for a predetermined period, and

(ii) records the net period for which the individual was actually in view during the total sampling period.

This method is especially suited to recording the rates at which events take place and also the duration of the various activity states of an animal (Altmann, 1974). It follows that the focal-animal must at all times of the sampling be instantly recognisable and clearly visible. In the case of wildebeest there are very few individuals which carry naturally distinguishable features or marks. To make certain that I was sampling the activity of the same wildebeest for periods of up to 14 hours, I marked a total of 60 individuals during the year of sampling. Yellow neckbands numbered in black from "1" to "60" were put on wildebeest which had been temporarily immobilised.

Ideally, a sufficient number of focal-animals should be sampled to represent the major age-sex groups of the population. Consequently, wildebeest were marked according to their natural social status or groupings. Calves up to one year of age, having undeveloped horns,

would lose neckbands. Their rapid growth rate also precluded the fitting of a constrictive device and so I sampled calves only when some natural aid made individuals recognisable. The sex-age and social classes used in this study and the number of individuals marked in each class are given in Table 4.1.

As an aid to recording the activity of a focal-animal and its immediate environmental conditions, I wrote a check list which was referred to for each sampling period. After initial trial samplings to acquaint myself with field conditions and procedure, I decided to employ a standard sampling period of 15 minutes every alternate 15 minutes. Thus every hour was equally divided as follows : 0-15 minutes (sample), 15-30 minutes (rest), 30-45 minutes (sample), 45-60 minutes (rest). The reason for choosing a 15-minute sampling period was that it constituted the maximum period that I could monitor efficiently using a stop-watch. Furthermore, 15 minutes (900 seconds) provided a rounded total for later calculating and analysing results, which was done in units of one second. Since it was not practical or possible to undertake lengthy, uninterrupted recordings of the activity of a free-ranging wildebeest with the aid of a stop-watch, my basic assumption was that a sampling period every alternate 15 minutes in effect monitored 50 % of

Table 4.1 : Major age-sex and social classes of wildebeest marked for the focal-animal study at Etosha (1977 - 78)

Class	Number of Individuals Marked with a Neckband
Lone, adult, territorial bull	19
Adult, territorial bull with mixed herd	2
Adult bull in bachelor herd	11
Immature and sub-adult bull (1-3 yrs) in mixed herd	7
Adult cow in mixed herd	15
Immature and sub-adult cow (1-3 yrs) in mixed herd	6
Total	60

total activity. Because of the strict schedule imposed by sampling exactly for 900 seconds, followed by a non-sampling (rest) period of exactly 900 seconds, I concluded that I would obtain, on average, a highly representative sample, namely 50 % of the wildebeest's activity between sunrise and sunset.

The data for each sampling period were recorded on tape in the field and later transcribed onto Fortran coding sheets. The field check list and an example of a completed coding sheet giving data for a 12-hour period (24 samples of 15 minutes each) are shown in Appendices 4 and 5 respectively. Appendix 4 is self-explanatory; however, I want to point out certain practical considerations for applying this method. All temperatures were measured at approximately one metre above the ground and sun temperature was recorded on a black bulb thermometer to simulate the heat absorptive pelage of wildebeest. To locate the sampling area a map grid size equivalent to 3,25 km^2 in the field was used. I obtained this grid size by dividing the degrees of longitude and latitude on a 1:500 000 scale map of Etosha into the greatest number of equal sized squares which could be practically referred to, namely 32 x 32 per 1 ^{o} longitude x 1 ^{o} latitude. I subjectively determined horizontal visibility by selecting one of five categories of distance that the focal-animal could see clearly, in relation to

predator cover. Also included in each sample was my assessment of whether the focal-animal had been unnaturally disturbed by myself or by vehicles over which I had no control. This was an indicator of whether the activity recorded could be regarded as natural or not. In this regard wildebeest clearly indicated when the distance was too small. Consequently, on the open plains of Etosha, I found 200-500 metres to be a practical viewing distance. All data on focal-animals were collected by myself, using a four-wheel drive vehicle. The tape recordings were transcribed onto Fortran coding sheets by a second person within a day, so that any points of confusion on the tape could be clarified. The volume of data collected during a study of this type made it essential that unprocessed data did not accumulate.

4.2.2 Instantaneous Scans of Herds

In contrast to focal-animal sampling the "instantaneous scan" is designed to record the current activity of one or more individuals at preselected moments in time (Altmann, 1974). "Scanning" is therefore a sampling of states, not events. It gives information on the time distribution of behavioural states in a group of animals and, in particular, on their behavioural synchrony. To scan wildebeest herds at Etosha, I distinguished between

bull herds and mixed herds. A standard scanning procedure was set which required one scan of the herd at 5-minute intervals, repeated 10 times every hour. This allowed a 15-minute interval for rest before commencing the next hour's sampling. At each scan, the age and sex class of all individuals in the herd, as well as each one's current activity, was recorded on tape. It was a prerequisite of this method to scan each individual for the same, brief period of time, failing which the scan sample became equivalent to a series of short focal-animal samples (Altmann, 1974).

Similar to the procedure for focal-animal sampling, I used a field check list (Appendix 6) and the tapes were transcribed onto Fortran coding sheets. Environmental data were recorded at 30-minute intervals. Because the data collected during each scan occupied more than the 80 coding columns available on each Fortran coding sheet, column 1 was reserved for the numerals "1" and "2". When these were used in conjunction with columns 2 to 10 (year, month, day, hour, minute), they formed a code unique to each scan which linked Statement "1" to Statement "2" and made them distinctly recognisable.

4.2.3 Monthly Schedule of Sampling and Sample Size

Each month, for a period of 13 months (May 1977 to May 1978), I attempted to sample four focal-animals from different major age-sex classes, namely adult bull, adult cow, immature bull, immature cow. No sampling was done in November and on two occasions (May 1977) I failed to locate a marked immature bull or an immature cow. In total 43 days and one night were spent recording the activity of a focal-animal from sunrise to sunset and, on one occasion, sunset to sunrise, for periods of 10 to 14 hours per age-sex class. During the dry, cold season (May to August) it was possible to follow focal-animals for unbroken periods of 10 hours. However, during the dry, hot season (September to December) high temperatures made it preferable to follow a focal-animal for up to seven hours (sunrise to midday) and then interrupt sampling until the following afternoon (midday to sunset). The wet, hot season (January to April) required up to three days to obtain an effective diurnal sample, due largely to heavy rain making it impossible to drive across the veld. On one occasion I followed an adult bull from sunset to sunrise for a period of 14 hours.

For the focal-animal study a total of 1 053 sample periods of 15 minutes each were recorded, or 263,25 hours. Total

focal sampling time was therefore 947 700 seconds, of which 947 234 seconds were net viewable time. Only 466 seconds of activity were not recorded when the focal-animals were lost to sight. This high percentage of viewable time (99,95 %) was due to the excellent visibility on the open plains of Etosha. Similarly, I carried out two scans per month : one on a bull herd and one on a mixed herd. Twenty days and four nights were used for this sampling, during which a total of 2 515 diurnal scans, involving 54 973 individuals, and 490 nocturnal scans, involving 11 717 individuals, were made. Scanning therefore accounted for 66 690 classifications of individual activity.

4.2.4 Data Analyses

The focal-animal and instantaneous scan data, as well as the environmental parameters recorded, were stored in a Univac 1106 computer. Focal-animal data were sorted to present sampling on a 15-minute, hourly, daily and monthly basis. The format for presentation is shown as an example in Table 4.2. Scan data were similarly analysed. Table 4.3 gives the format used. Two separate ANOVA for the focal and scan data respectively, were obtained from the computer. Additional statistical tests (t-test, Chi-square and linear regression) were done using a Hewlett-Packard 25C electronic calculator which was programmed to execute these statistics.

Table 4.2 : Format presented on computer printout of one 15-minute focal-wildebeest activity sample at Etosha

DATE: 7-06-08
TIME: 08H30

VIEWABLE TIME : 900 TOTAL FOCAL SAMPLING TIME : 900
CLOUD COVER : 0 WIND SPEED : 2 WIND DIRECTION : 2
SHADE TEMP : 15 SUN TEMP : 16
DAILY RAINFALL : 0 MM RELATIVE HUMIDITY : 30
MAP GRID : 67-18 HORIZONTAL VISIBILITY : 5
VEGETATION TYPE : 3 VEGETATION HEIGHT : 3
INFLUENCE OF OTHER SPECIES : 0
UNNATURAL DISTURBANCE : 0
DISTANCE MOVED : 5
DISTANCE FROM OTHER WILDEBEEST : 0
DISTANCE FROM OTHER HERBIVORES : 2
OTHER OCCURRENCES : 0
AGE - SEX : 8

	%	Total
RESTING (LYING)	0,0	0
RESTING (STANDING)	3,5	32
GRAZING (STATIONARY)	41,9	377
GRAZING (MOVING)	26,1	235
WALKING	26,7	240
TROTTING	0,0	0
GALLOPING	1,8	16
SHADING (LYING)	0,0	0
SHADING (STANDING)	0,0	0
DRINKING (SEASONAL)	0,0	0
DRINKING (PERENNIAL)	0,0	0
SUCKLING	0,0	0
SOCIAL ENCOUNTERS	0,0	0
TOTAL TIME (IN SECS)	100,0	900

Table 4.3 : Format presented on computer printout of one 5-minute interval scan of a wildebeest herd at Etosha

SCAN NUMBER 245

DATE: 7-06-13 TIME: 08-25 PLACE: 66-19 NUMBER: 23 SCAN TIME: 24 SECS

WIND: 03 RAIN: 00 TEMP: 13 VEG TYPE: 03 VEG HT: 03 UNNAT DISTB: 00 DIST MOVED: 01

ACTIVITY	ADULTS MIXED		BULL BACHELORS		JUVENILES		UNIDENTIFIED	
	BULL	COW	ADULT	IMMATURE	2ND YEAR	1ST YEAR	? SEX-AGE	ADULT ? SEX
RESTING	0	1	0	0	0	0	0	1
GRAZING	1	10	0	0	4	6	0	0
MOVING	0	1	0	0	0	0	0	0
IN SHADE	0	0	0	0	0	0	0	0
DRINK SEASONAL-WATER	0	0	0	0	0	0	0	0
DRINK PERENNIAL WATER	0	0	0	0	0	0	0	0
DRINKING						0		
SUCKLING						0		
SOCIAL ACTIVITIES	0	0	0	0	0	0	0	0

4.3 ANALYSES OF ACTIVITY

4.3.1 Comparison of Focal and Scan Data for a Total of One Year

Since the methods for collecting focal-animal and instantaneous scan data were basically different, a comparison of their gross results over a period of one year indicated whether they had been applied successfully. If the two sets of results were in close agreement, then it would suggest that they each were a valid means of sampling the activity patterns of wildebeest. Table 4.4 compares the percentage gross diurnal activity of wildebeest at Etosha using the data collected for all the focal-animal samples and all the instantaneous scan samples.

4.3.1.1 Resting and Grazing

There was a difference of 1,2 % in the case of resting and 0,4 % in the case of grazing activity recorded. These differences are so slight, if account is taken of the basically different sampling methods, the periods of sampling, and the number of samples, that the results can be considered equal for the year under comparison.

Table 4.4 : Comparison of focal-animal and instantaneous scan methods : percentage gross diurnal activity of wildebeest at Etosha

Period	Criterion Used	Percentage Activity						
		Resting (Lying, standing, shading)	Grazing (Stationary, walking)	Movement (Walk, trot, gallop)	Drink Seasonal Water	Drink Perennial Water	Suckle	Social Encounters
May 1977	Focal-animal study	52,9	32,0	13,8	0,1	0,2	0,1	0,9
to								
May 1978	Instantaneous scan of herds	54,1	32,4	11,7	0,1	0,2	0,1	1,4

4.3.1.2 Drinking Water and Suckling

The two methods showed identical results and it is interesting to note that sampling was sensitive enough to reflect a difference between the availability of water. At Etosha the seasonal rainwater was available to wildebeest for approximately four months of the year (the wet, hot season from January to April). They then drank it exclusively, by preference. During the remaining eight months (the cold, dry and hot, dry seasons), water was limited to perennial fountains. The time ratio of 1 : 2 imposed by the availability of different water sources was exactly reflected in the frequency at which wildebeest drank from them.

4.3.1.3 Movement and Social Encounters

Although the differences were slight : 2,1 % in the case of movement and 0,5 % in the case of social encounters, they were proportionately greater than the differences in other activity categories. My assessment is that the observations I made on these two activity categories was biased, favouring "movement" at the expense of "social encounters" in the focal study. This bias probably resulted from the arbitrary point in time where I decided that "movement, unrelated to intra-specific social

behaviour" had changed to the subtly linked category of "social encounters". To illustrate this point let me give the example of an adult bull wildebeest which was patrolling its territory. According to the definition of category, the bull was engaged in non-social movement. However, at a point in time indiscernible to me, the bull detected a potential rival on an adjoining territory and commenced moving towards the rival. Strictly speaking, the bull had entered the social encounter phase of activity, but was still being recorded as "moving". Only when the bull commenced obvious territorial or threat displays did I record that the focal-animal was in social encounter. Thus I recorded time against "movement" at the expense of "social encounter". The requirements of focal-animal sampling, namely to watch all activity of one animal, may have therefore prevented me from seeing that a second animal was entering the scene and was affecting the animal being watched. If we now consider the greater latitude which scanning a herd afforded, it is easy to understand that a "social encounter" situation will be noticed sooner, since the scan method required that all animals be checked briefly for current activity.

I am therefore of the opinion that the scan data for the activity categories of "movement" and "social encounters" are more realistic than those recorded by the focal-animal

data. However, for the purpose at which this exercise was directed, namely to obtain baseline data on activity and extrapolate an energy budget from it (Section 5), the different methods' data are within acceptable limits.

4.3.2 Comparison of Focal and Scan Methods by Season

To further verify that the methods for collecting data on activity were valid, I compared the focals and scans on a seasonal basis (Table 4.5). The percentage activity in each category was compared statistically, using the paired t-statistic. Data for each of the seasons was paired for this purpose. The t-test is sufficiently robust to allow the use of percentages in testing for significant differences (Sokal and Rohlf, 1969). No statistically significant differences were found in any of the seven activity categories used for focals and scans ($P > 0,05$).

4.3.3 Comparison of Focal and Scan Methods by Month

The test for validity of the methods was extended to the monthly level (Table 4.6), using the t-statistic for two means. Again, no statistically significant differences were found in any of the seven categories used for focals or scans ($P > 0,05$).

Table 4.5 : Comparison of focal and scan methods : percentage of time, on a seasonal basis, spent by all age-sex classes of wildebeest combined, in seven different activity categories

Season	Criterion Used	Percentage Activity						
		Resting	Grazing	Movement	Drink Seasonal Water	Drink Perennial Water	Suckle	Social Encounters
Wet, hot (January to April)	Focal	55,9	31,0	11,2	0,2	-	0,3	1,4
	Scan	49,3	38,7	9,7	0,2	-	0,1	2,0
Dry, cold (May to August)	Focal	55,6	29,2	13,8	-	0,3	0,1	1,0
	Scan	54,1	32,4	12,0	-	0,2	0,1	1,2
Dry, hot (September to December)	Focal	45,2	36,7	17,3	0,1	0,3	0,1	0,3
	Scan	60,1	26,8	12,2	-	0,3	-	0,6

Table 4.6 : Comparison of focal and scan methods : percentage of time, on a monthly basis, spent by all age-sex classes of wildebeest combined, in seven different activity categories

Month	Criterion Used	Percentage Activity						
		Resting	Grazing	Movement	Drink Seasonal Water	Drink Perennial Water	Suckle	Social Encounters
January 1978	Focal	33,8	52,1	13,3	0,3	-	0,2	0,3
	Scan	40,0	48,3	11,2	-	-	0,1	0,4
February 1978	Focal	66,3	23,5	8,6	0,1	-	0,6	0,9
	Scan	44,8	44,2	9,3	0,2	-	0,2	1,3
March 1978	Focal	68,4	21,0	8,9	0,1	-	0,3	1,3
	Scan	59,1	27,9	8,8	0,3	-	0,1	3,8
April 1978	Focal	55,3	27,6	13,8	0,2	-	0,2	2,9
	Scan	64,0	22,0	10,2	0,6	-	0,1	3,1
May 1978	Focal	47,6	34,0	17,4	-	0,5	0,1	1,4
	Scan	41,1	36,3	19,9	-	0,1	0,1	2,5
June 1977	Focal	60,2	28,7	8,7	-	0,2	-	2,2
	Scan	51,1	31,9	16,7	-	-	-	0,3
July 1977	Focal	59,3	24,2	15,9	-	0,3	0,1	0,2
	Scan	65,6	27,9	5,9	-	0,1	-	0,5
August 1977	Focal	61,3	28,4	9,9	-	0,2	-	0,2
	Scan	59,1	32,8	7,3	-	-	-	0,8
September 1977	Focal	52,9	36,3	9,9	-	0,5	-	0,4
	Scan	50,9	36,3	11,4	-	0,6	-	0,8

Table 4.6 (continued)

Month	Criterion Used	Percentage Activity						
		Resting	Grazing	Movement	Drink Seasonal Water	Drink Perennial Water	Suckle	Social Encounters
October 1977	Focal	50,4	26,4	22,5	-	0,5	0,1	0,1
	Scan	56,8	31,0	10,6	-	0,4	-	1,2
November 1977	-	No data collected						
December 1977	Focal	32,6	47,6	19,5	0,1	0,1	-	0,1
	Scan	67,2	17,0	15,6	-	0,1	-	0,1

4.3.4 Simultaneous Application of Focal and Scan Methods

A simultaneous sampling of the activity of a focal-animal and the activity of the herd of which it is a member, by scanning, should produce comparable results. This assumption is valid providing :

(i) there is a synchrony in the herd's activities;

(ii) the herd sampled is reasonably homogeneous in regard to age-sex class; and

(iii) the focal and scan methods are correctly applied.

Synchrony within wildebeest herds can be quantitatively demonstrated and I will discuss this aspect later (Section 4.3.7). The reason for sampling from an homogeneous herd is to minimise the possibility of the focal-animal deviating significantly in its activity from the rest of the herd due to its particular age-sex class. To illustrate this point, consider the very different activity regime of a territorial bull during the rut in comparison to the mixed herd of cows and immatures he has claimed. Obviously then, the ideal herd to sample for this purpose will be a bachelor herd of adult bulls.

To test my methods simultaneously, I selected wildebeest

herds of exclusively adult bulls on two consecutive days. On the first day 10 bulls were followed from 06h30 to 13h30 and on the second day a different herd, varying between 10 and 22 bulls, was followed from 13h30 to 19h30. The results obtained are illustrated on an hourly basis and as a mean in Fig. 4.1. Although the results could not be compared statistically by Chi-square because the nature of sampling required that percentages be calculated for comparison (Sokal and Rohlf, 1969), the differences were small. Individual variation in the activities of animals has been found to occur in even the most visually homogeneous herds (Sinclair, 1977). The important fact which emerged from this experiment was that sampling the activity of a wildebeest, and probably any other ungulate, for too short a period, will give variable results. For example, on one occasion during the experiment (10h00 - 11h00), the focal-animal rested for 0,8 % of an hour, while the herd rested 15,0 %. Conversely, during the following hour, the focal-animal rested 5,7 % of the time, while the herd rested 2,0 %.

To make conclusions about the diurnal activity patterns of wildebeest, based on only part of the day, is therefore obviously invalid. Support for this statement is given by Fig. 4.1 which graphically compares not only focal and scan methods by hour, but also as a mean of the day. The

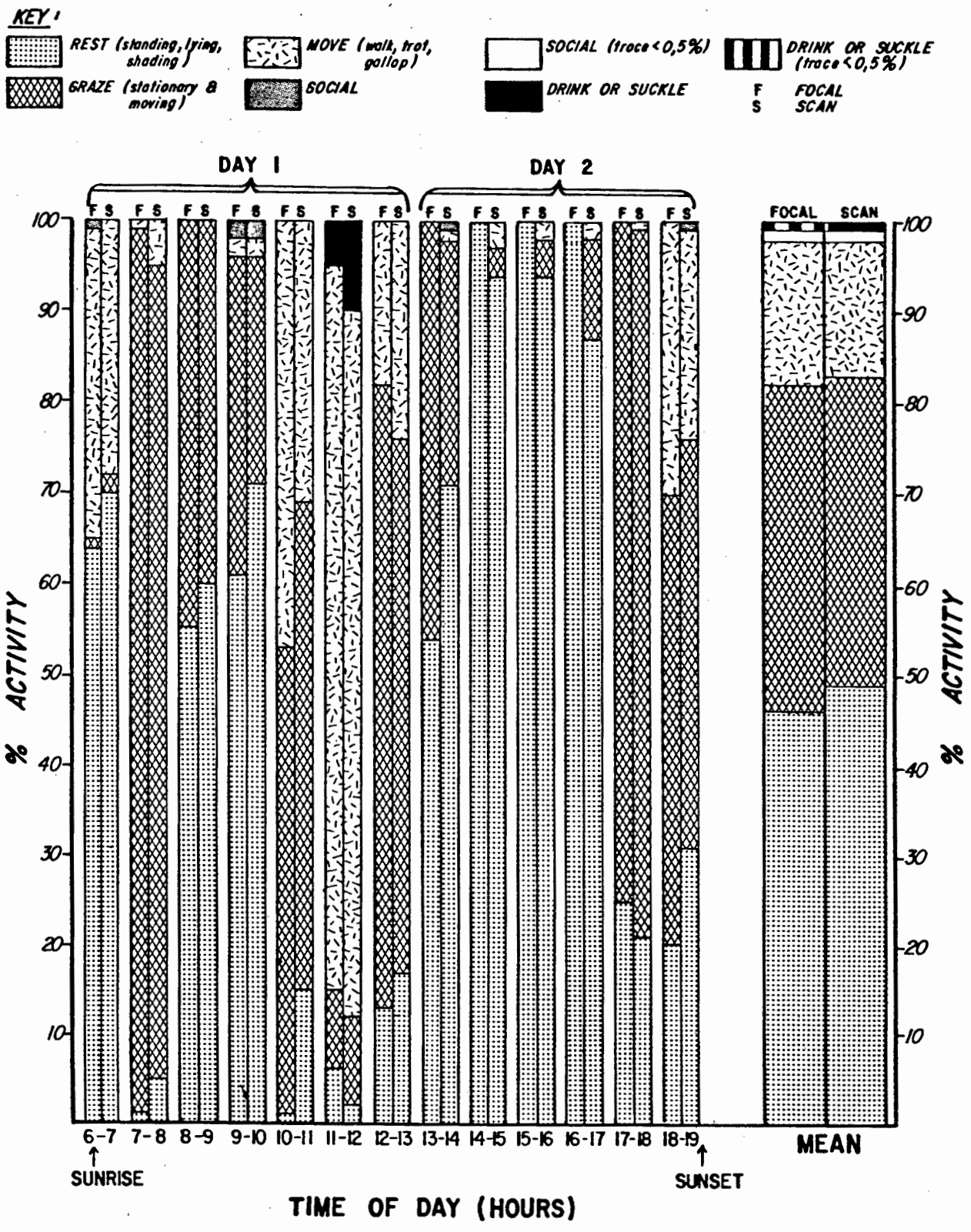

Fig. 4.1 : Comparison of the simultaneous application of focal and scan methods to determine the activity of adult bull wildebeest.

mean represents an equally-spaced sample of 50 % of the total activity of a focal-animal from sunrise to sunset. The mean for the scan represents 2 186 individual classifications of activity for 100 % of the herd at a rate of 10 scans per hour, during the entire diurnal period. Based on this diurnal mean, there is only 3 % difference in resting, 1 % difference in grazing and movement, and negligible differences in the drinking of water and social activity.

4.3.5 Focal-animal Studies

The volume of data obtained from the study of focal-animals precluded the presentation and discussion of all the detail. Instead, I have chosen to collate the diurnal activity patterns of wildebeest on a yearly and seasonal basis for the population. As an example of diurnal and nocturnal activity of an individual, the time-related behaviour of a territorial bull in a mixed herd is discussed. The environmental parameters attending the activity of wildebeest at Etosha have been similarly collated. Two environmental parameters especially, have a bearing on the activity and associated behaviour of wildebeest, namely photoperiod and ambient temperature. Diurnal activity appeared to be directly correlated to prevailing temperatures and will be discussed here.

Photoperiod will be discussed in relation to diurnal and nocturnal activity (Section 4.3.6.4).

4.3.5.1 Yearly Diurnal Activity Patterns of the Population

Fig. 4.2 presents diurnal activity patterns of the wildebeest population at Etosha. The histogram takes into account all major age-sex classes (Section 4.2.3) and the immature wildebeest included samples of calves, yearlings and sub-adults. A more detailed explanation of these age-sex classes and their respective activities is provided by month in Appendix 7. The annual variation in photoperiod was accounted for by correcting all sampling times to number of hours after sunrise on the X-axis. I propose to discuss each of the five major activity classes and their components separately, referring briefly to activities which were linked.

(a) Resting

The mean diurnal resting time was 52,9 %. Of this, the majority (31,5 %) was spent lying in a sternal position. Resting in a standing position accounted for the remaining 21,4 %. Resting reached its lowest level immediately after sunrise when wildebeest usually moved away from the area occupied at night and commenced grazing. Ambient

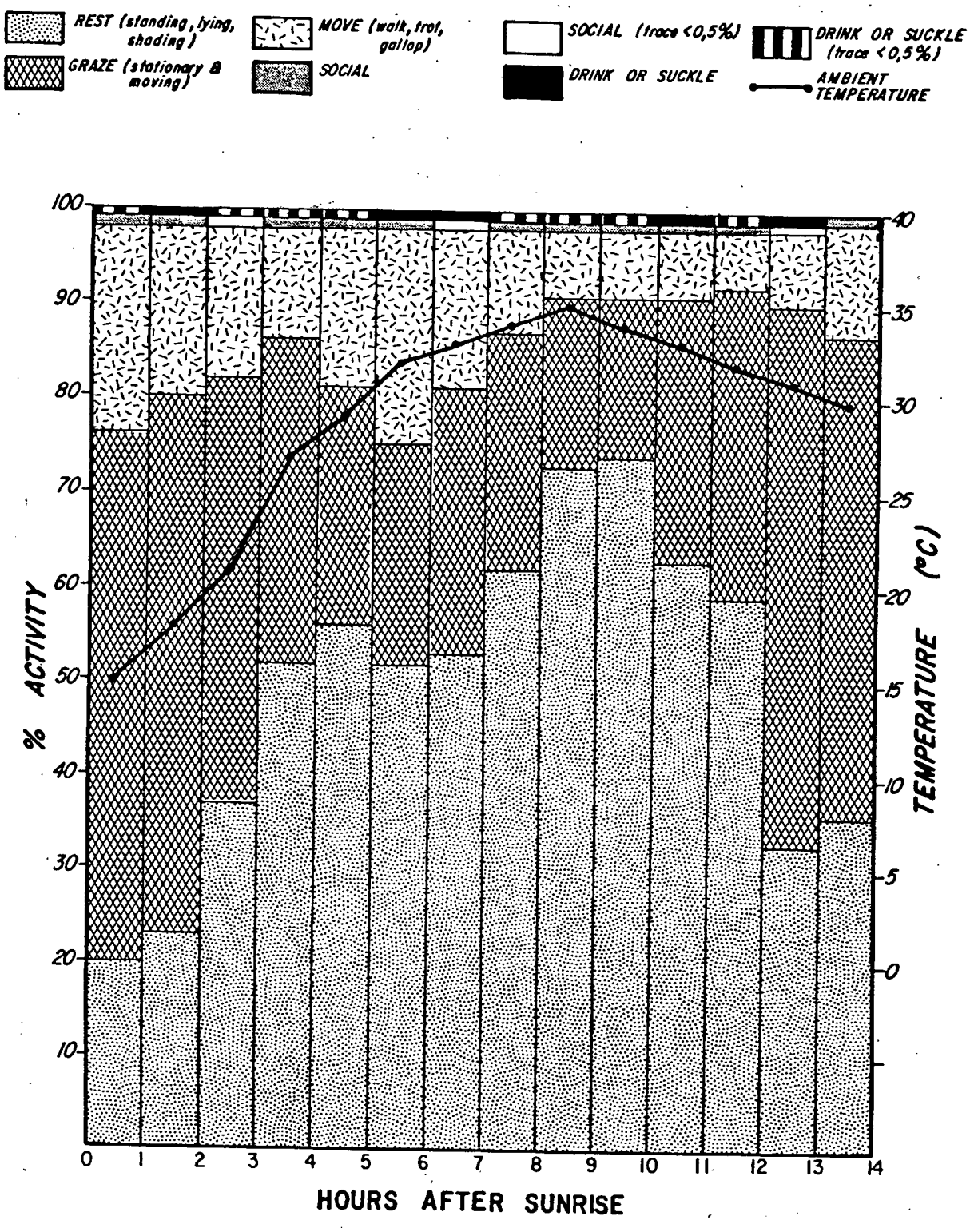

Fig. 4.2 : Yearly diurnal activity patterns of the wildebeest population and mean ambient temperatures at Etosha, using the focal animal method.

temperature was also at its lowest during this period. Thereafter, both resting and temperature increased to a point where 52 % of the population rested at a mean temperature of 27 ^{o}C. Five to six hours after sunrise, there was a slight decrease in resting when most wildebeest moved to drink water. This activity was followed by a sharp increase in resting which coincided with the highest diurnal mean temperatures. Within an hour or two of sunset, as temperatures dropped, there was an appreciable drop in resting behaviour. It seems very plausible to link the regimes of temperature and wildebeest resting, since the heat-absorptive pelage of wildebeest would certainly require the animal to decrease its activity at high temperatures (Leuthold, 1977; Jarman and Jarman, 1973). The term "heat load" has been used to describe this phenomenon (Lewis, 1975).

To determine statistically whether a relationship existed between increasing temperatures and the percentage of wildebeest resting, I applied a linear regression equation by the method of least squares (Zar, 1974). I calculated ascending temperature against the percentage of wildebeest resting from nil to nine hours after sunrise (mean temperature range = 15 ^{o}C - 35 ^{o}C). The linear regression equation is $Y = 0{,}04X + 8{,}02$ ($r = 0{,}91$) and gave a good fit to the data (Fig. 4.3). The correlation coefficient

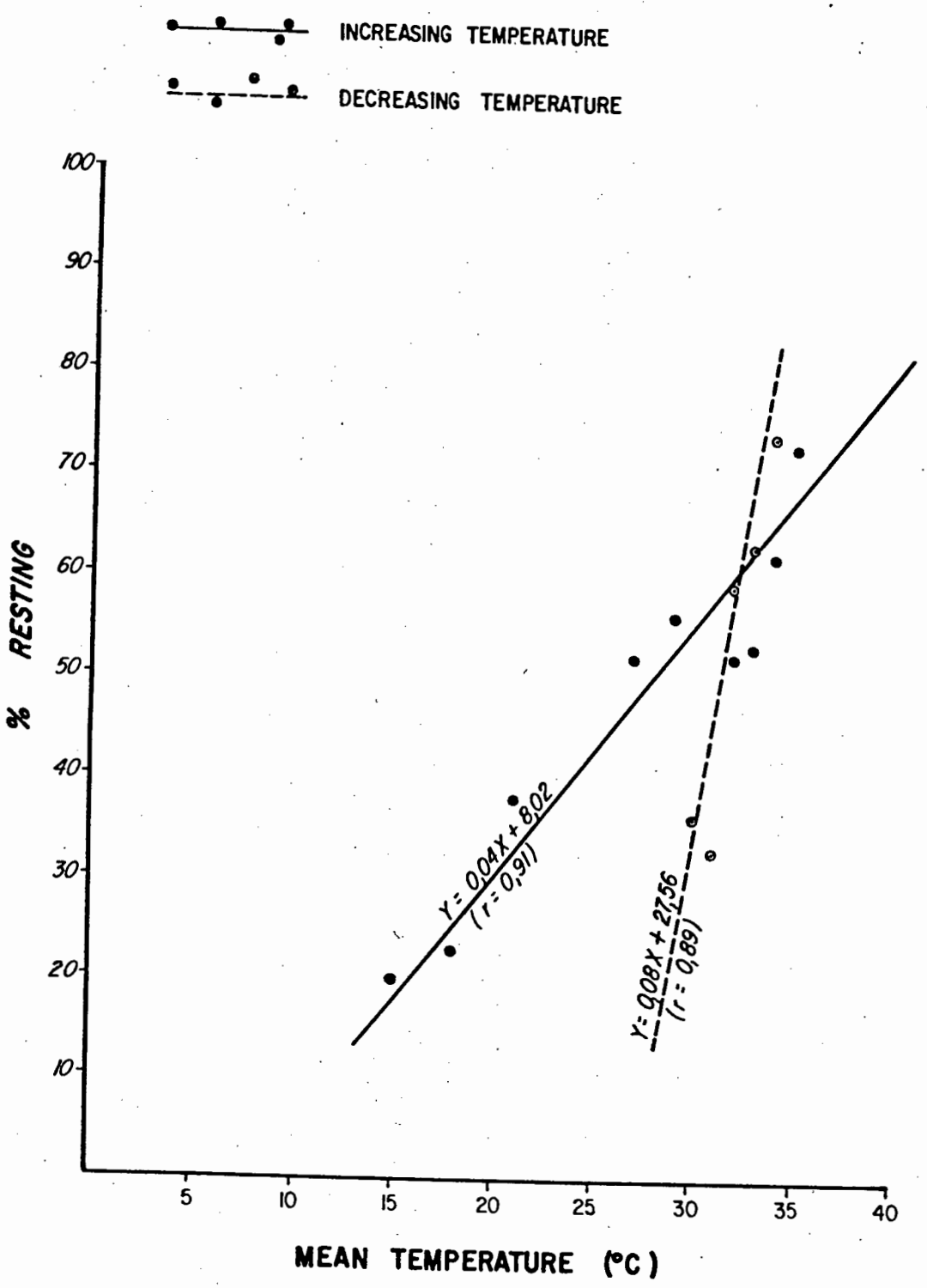

Fig. 4.3 : Relationship between mean ambient temperature and percentage of wildebeest resting, on a yearly basis, at Etosha.

is 0,95 ($P < 0,01$). Conversely, when temperatures declined, wildebeest became more active and I calculated declining temperature for the last five hours of daylight (34 ^{o}C - 30 ^{o}C) against percentage of resting animals. The resultant regression equation is linear : $Y = 0,08 + 27,56$ ($r = 0,89$) and is included in Fig. 4.3. The correlation coefficient is 0,94 ($P < 0,01$). The ascending and descending temperature regimes were therefore well correlated with the incidence of inactivity in wildebeest at Etosha.

(b) Grazing

Food intake in ruminants, although having peaks in intensity, is a continual process because of the specialised feed/ruminating routine (Leuthold, 1977). However, he is of the opinion that an early morning/late afternoon feeding peak with a lengthy midday period of inactivity for wild ruminants is an over-simplification. Because quantitative data on foraging activity of free-ranging African ungulates are scant, the following findings on wildebeest at Etosha may provide further insight into this.

On average, the wildebeest population spent 32 % of diurnal time grazing, of which 27,9 % was stationary, intensive foraging and 4,1 % was grazing interspersed with purposeful

walking. The majority of time (57 %) of the first two hours after sunrise was occupied by grazing. This declined to 23 % during the following four hours, followed by a slight increase when the majority of wildebeest moved to drink water. It was, however, not intensive foraging. The animals typically snatched at grass tufts as they moved purposefully to drink. There was a brief period of less than an hour after drinking during which wildebeest grazed intensively. This appeared to be a "topping-up" phase and preceded the lengthy mid-afternoon resting/ruminating period. Food intake by the population never completely ceased, because there were always wildebeest whose age class or reproductive status required that they forage while the majority rested. The least grazing (17 - 18 %) was during the mid-afternoon period and occupied about two hours, when ambient temperatures were at a maximum. Thereafter grazing time rapidly increased as temperatures declined and the late afternoon peak was remarkably similar (52 - 58 %) to the early morning peak of grazing.

I was unable to approach wildebeest closely enough to quantitatively determine their bouts of rumination. Nevertheless, rumination was observed throughout the day, when animals rested. A prolonged period of ruminating occurred in buffalo at dawn and again in the early evening (Sinclair, 1977) while the ratio of ruminating to grazing

increased in the dry season due to the increase of fibre content (Sinclair, 1974). Female impala showed a feeding : ruminating ratio varying between 1,83 : 1 and 3,67 : 1 during diurnal studies conducted from January to July (Jarman and Jarman, 1973). David (1978b) found that territorial springbok rams spent 11,4 % ± 9,6 % of their diurnal time in rumination. My casual observations showed two peaks of rumination during the day, both co-inciding with periods of prolonged rest. The first occurred three to five hours after sunrise, suggesting a time-lag of two hours after the early morning peak of grazing. The second occurred during a much longer period (8 - 12 hours after sunrise) and followed drinking and grazing with a similar time-lag.

Grazing was second to resting in the time it occupied for wildebeest at Etosha. Approximately one-third of the day was spent foraging, while more than half was spent resting. This supported my hypothesis (Section 4.4.2) that, during the study period, food or foraging did not appear to be limiting factors for the wildebeest population.

(c) Movement

Movement occupied, on average, 13,8 % of the wildebeest's diurnal activities. Walking comprised nearly all of this

(13,1 %), while trotting (0,1 %) and galloping (0,6 %) occurred in insignificant amounts. Trotting took place mostly during bouts of social encounters and in the play periods of young calves. Galloping was recorded mostly during the rut when bulls patrolled their territories intensively. It was also a feature of behaviour when wildebeest approached water and, of course, when they encountered predators.

Two daily peaks of movement became apparent during this study : the first at sunrise when herds moved to a preferred grazing area; the second about five hours after sunrise when going to and returning from water. In both these periods movement occupied 23 % or nearly double the average time. The least movement occurred between early and late afternoon, a period of five hours, when only 6 % - 8 % of total time was spent in movement. During the hour preceding sunset there was an upsurge in purposeful movement when the wildebeest foraged. The major diurnal movements of wildebeest at Etosha were therefore to walk to and from water and in search of food. The seasonal variation of this activity will be discussed in Section 4.3.5.2.

(d) Social Encounters

On average, overt social encounters occupied about 1 % of the wildebeest's diurnal activity at Etosha. These bouts of social behaviour were spread evenly throughout the day and occurred at all times. During three of the 14 hours of observation, there was only a trace of obvious social activity (less than 0,5 %). Thus it is of interest to note that although the wildebeest is considered a gregarious animal and much work has been done on its social status in the wild (Estes, 1966, 1968, 1969, 1974), 99 % of its behaviour may be centred primarily on other activities. In this context, I considered the activities of resting, grazing, moving and drinking water to have no overt social overtones and to be socially passive periods, although they are carried out in a gregarious manner by members of a herd. Subtle social exchanges, which are not noticed by a human observer may, however, exist during these other activities. The exclusive nature of wildebeest herds has been mentioned by Estes (1966) and aspects of their synchrony studied (Sinclair, 1977). However, the extremely low incidence of overt social interactions in relation to total behaviour has not previously been measured in wildebeest.

(e) Drinking Water and Suckling

Although drinking was recorded during all hours of daylight, with the exception of the last hour before sunset, there was a definite preference to drink between five and seven hours after sunrise. This was approximately from 11h00 to 13h00 and is in agreement with Du Preez and Grobler (1977) who recorded that 95 % of wildebeest (n = 1 426) drank during the day.

When considered in relation to the activity associated with drinking, namely moving to and from water, it seems contradictory that wildebeest should choose midday for drinking. This was a time of increasing temperature and any movement was made at the expense of resting, an activity which minimised "heat load" (Lewis, 1975). The special conditions existing in Etosha, where water is limited for most of the year, have produced equally specialised conditions for predators of wildebeest, notably lions. Most perennial water sources have lions in attendance or lying-up nearby. It follows that the movement to and from waterholes, as well as the act of drinking, constituted the greatest period of exposure to predation for wildebeest. It is consequently logical that wildebeest prefer to drink when lions are inactive. A midday period of inactivity was the predominant

behaviour in free-ranging lions (Schaller, 1972 and personal observations) and is probably correlated with increased temperature.

Etosha's wildebeest have apparently adopted a strategy for drinking whereby the majority moved to and from water when ambient temperatures reduced predator activity. They thereby sacrificed valuable time to off-load heat by resting and other specialised behaviour such as panting and orientation to the wind. Predator evasion thereby overrides the thermoregulatory instinct. Nevertheless, this drinking schedule allowed wildebeest at Etosha to return to an area of relative safety and to commence the lengthy afternoon rest period before the highest temperatures occurred. The pattern of drinking activity was therefore well-adjusted to prevailing biotic and abiotic factors in the environment.

Suckling was included in this activity to simplify the results given in Fig. 4.2. Suckling was recorded whenever the focal-animal gave milk, as in the case of a lactating cow, or received milk, as in the case of a calf drinking from its mother. Peak diurnal suckling times were one to two hours after sunrise, towards midday, during mid-afternoon and about one hour before sunset. This pattern of suckling was especially obvious in calves younger than

three months. The focal-animals I observed suckled up to five times in a period of 13 hours. As in the case of adult drinking, suckling was seen in all daylight hours, although I did not record it during the last hour before sunset in the focal-animal studies. This may have been due to limited sampling.

4.3.5.2 Seasonal Diurnal Activity Patterns of the Population

Seasonal influences on the activity patterns of wildebeest at Etosha are presented in Figs 4.4 to 4.6, applying the same corrections for varying photoperiod. Since the general diurnal activity regime has been discussed in some detail in Section 4.3.5.1, I will only draw attention to significant departures from it which are probably due to seasonal changes.

(a) Wet, Hot Season (January to April)

The correlation coefficient for the relationship between increasing mean temperatures and percentage of wildebeest resting was significant (0,83; $P < 0,01$). The linear regression equation for this relationship is $Y = 0,45X + 3,91$ ($r = 0,69$). There was therefore a tendency for scatter of the data around the regression line and this was

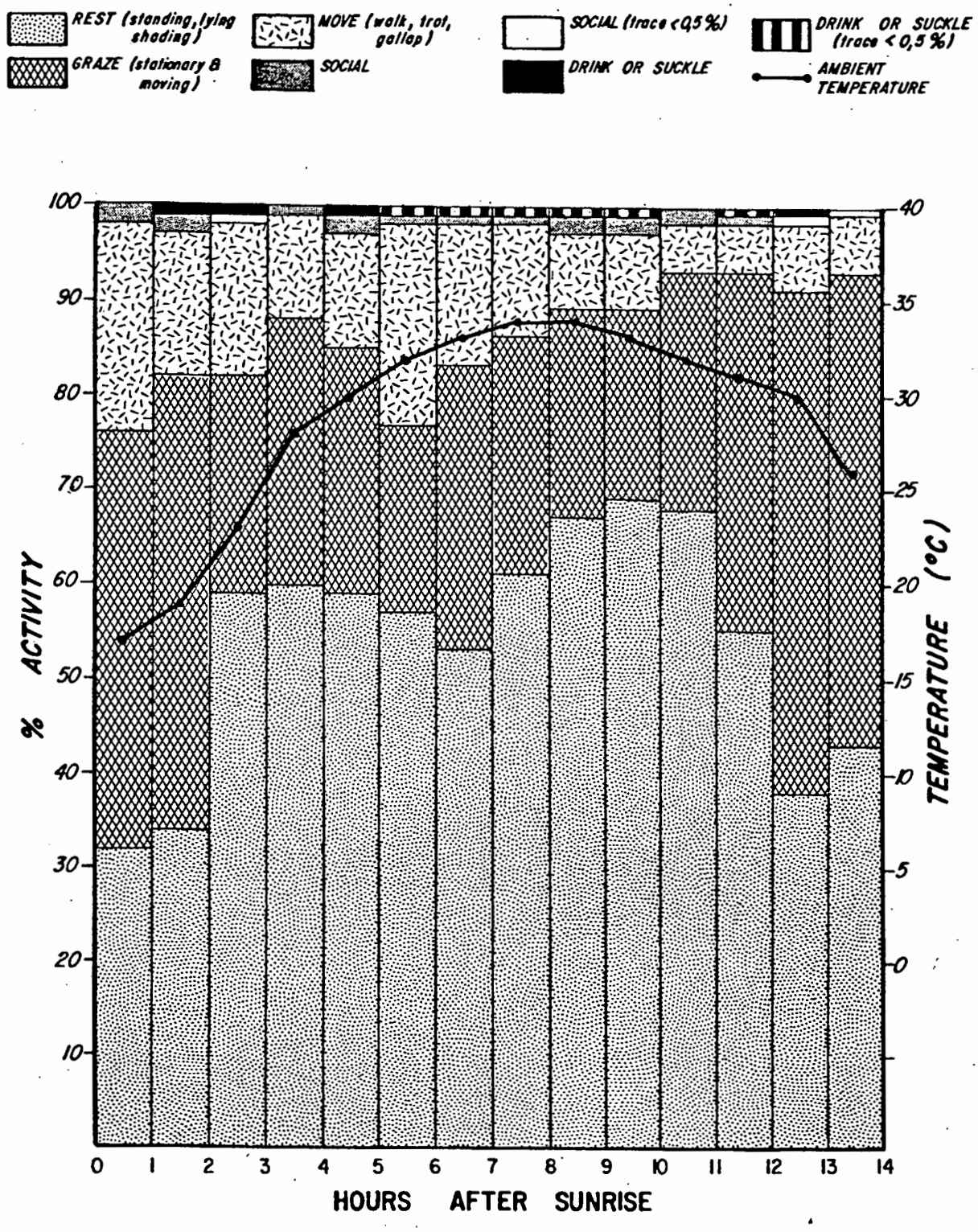

Fig. 4.4 : Diurnal activity patterns of wildebeest and mean ambient temperatures at Etosha during the wet, hot season, using the focal animal method.

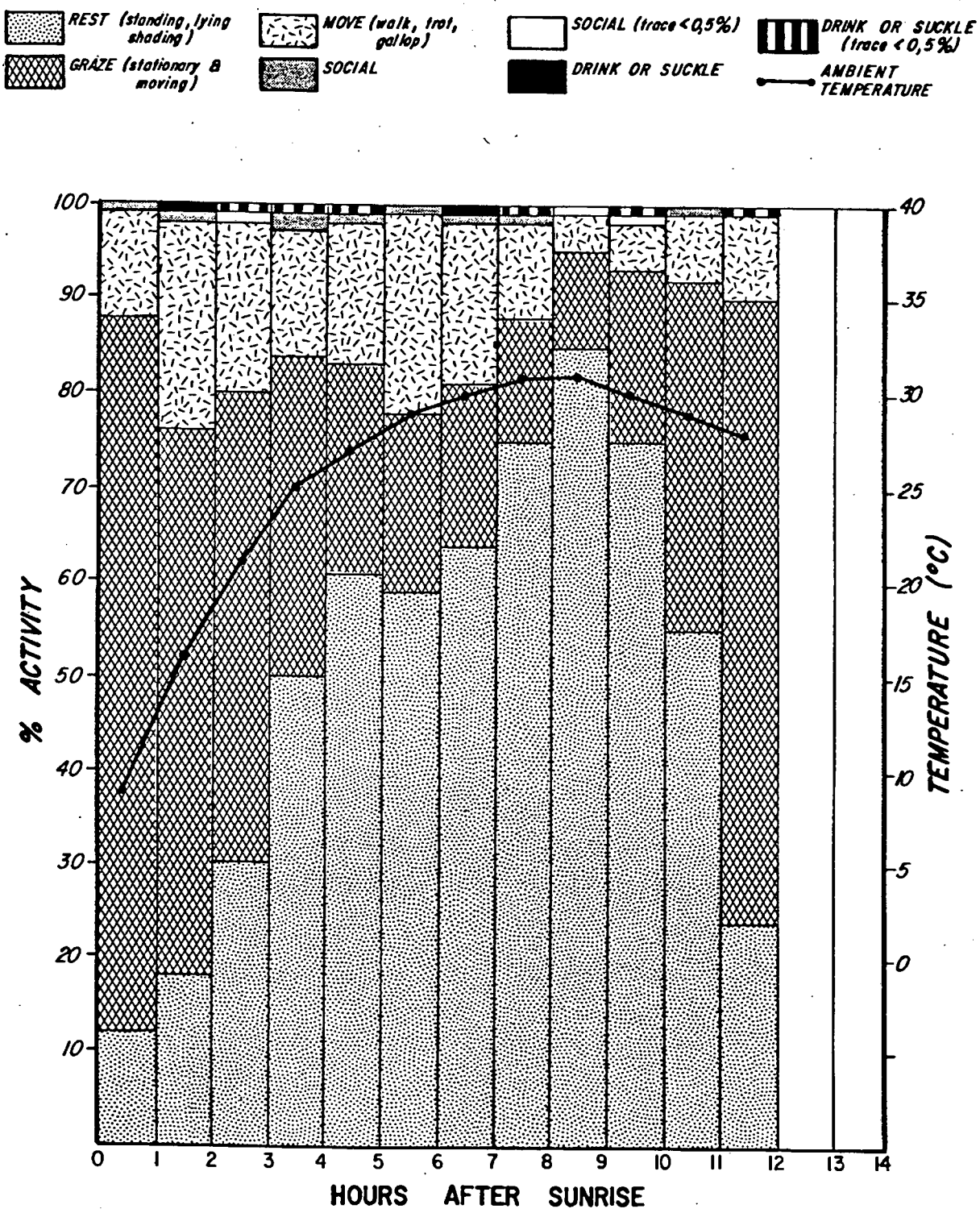

Fig. 4.5 : Diurnal activity patterns of wildebeest and mean ambient temperatures at Etosha during the dry, cold season, using the focal animal method.

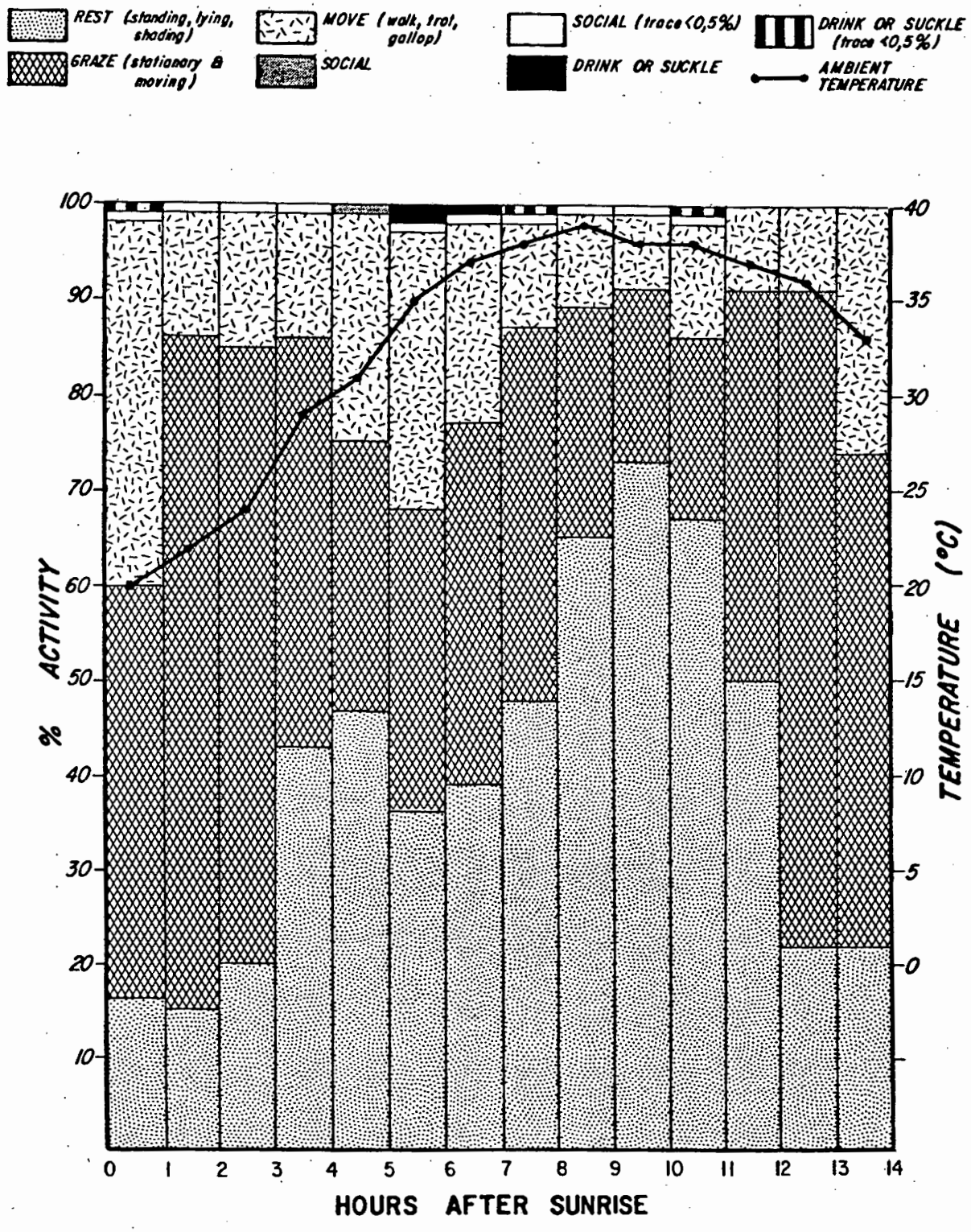

Fig. 4.6 : Diurnal activity patterns of wildebeest and mean ambient temperatures at Etosha during the dry, hot season, using the focal animal method.

probably due to the high percentage of wildebeest which rested early in the day during the hot season. A second environmental factor, namely increased relative humidity may have been related to this early resting period. For instance, relative humidity recorded at the time when resting activity increased sharply (2 - 3 hours after sunrise) showed a mean of 68 % (January), 80 % (February), 84 % (March) and 80 % (April). During the dry seasons (May to December) the relative humidity range was much lower (41 % - 68 %). The resting curve in Fig. 4.4 is decidedly broader and also less peaked than for the other seasons, although the total time spent resting (55,9 %) did not differ much from the yearly average (52,9 %). No correlation could be found between decreasing temperature and a decrease in percentage resting during this season ($r = 0,77$; $P > 0,05$). Grazing time was virtually the same as the yearly average, but movement was predictably less, due to the relative abundance of food and water. Two outstanding features of wildebeest activity during the wet, hot season were the increase in social behaviour as the rut commenced, and the increased frequency of suckling due to the calving period.

(b) Dry, Cold Season (May to August)

Fig. 4.5 shows marked grazing peaks in the early morning

and late afternoon, at the expense of resting. However, the total times allocated to resting and grazing differed very little from the wet, hot season or from the average for the year. There was a highly significant correlation coefficient (0,96; $P < 0,01$) between increasing temperature and percentage resting. The regression equation is $Y = 0,32X + 8,73$ ($r = 0,93$) and fits the data well. Similarly, the correlation coefficient for decreasing temperature on decrease in resting was 0,97 ($P < 0,01$) and the regression equation is $Y = 0,05X + 26,71$ ($r = 0,95$) with a very good fit of the data. To compensate for reduced resting time at the start and end of the day, wildebeest rested as much as 85 % of total time during mid-afternoon. Mean temperature at this time was 31 ^{o}C, which is only 4 ^{o}C lower than the corresponding mean for the year. There was an increase in time spent moving, compared to the wet, hot season and this was probably due to decreased availability of both food and water. Both social behaviour and suckling frequencies dropped in the dry, cold season. This corresponded to the end of the rut and increasing independence of the calves.

(c) Dry, Hot Season (September to December)

Fig. 4.6 shows the most marked deviation from the other seasons as well as from the yearly average. Total time

spent resting was reduced to 45,2 %, while time spent grazing increased to 36,7 %. Movement also reached its highest level (17,3 %) and more time was spent drinking. Both social behaviour and suckling were at the lowest level of the year. This change in activity was in accordance with demands made by the environment on the wildebeest. Food was still available, but more time was required to forage for it. Thus grazing and movement increased at the expense of resting. Likewise, water was very limited in distribution and this was reflected in the pronounced midday decline in resting and accompanying increase in movement to perennial waterholes. There was nevertheless a significant correlation between increase in temperature and rest (correlation coefficient was 0,86; $P < 0,01$). The regression equation is $Y = 0,37X + 16,90$ ($r = 0,73$) with a reasonable fit to the data. Similarly, decrease in temperature was significantly related to decreased resting (correlation coefficient 0,85; $P < 0,01$). The regression equation is $Y = 0,07X + 33,01$ ($r = 0,72$) and fits the data reasonably.

4.3.5.3 Diurnal and Nocturnal Activity of a Territorial Bull in a Mixed Herd

The activity of a territorial bull wildebeest has been chosen for discussion because it was the only age-sex

class on which I was able to obtain diurnal and nocturnal data using the focal-animal method. In August I followed a neckbanded bull for an unbroken period of 10 hours from sunrise to sunset and in September I followed the same individual continuously for 14 hours from sunset to sunrise. The data are presented on an hourly basis in Fig. 4.7 and the means for the total diurnal and nocturnal activity are compared. I allowed one hour's overlap at the beginning and end of the observations and so 25 hours were recorded in total.

Four resting peaks (> 75 %) were evident, three of them occurring at night, while a fifth, less pronounced, resting period took place from mid-afternoon to sunset. There was a period of one to three hours between these resting periods which was mostly devoted to grazing. Four peaks of grazing were discernible : sunrise to mid-morning, late afternoon - early evening, approaching midnight, and the early morning hours. Three definite periods of movement occurred. The major movement was to and from water at midday, while noticeable movement took place at sunrise when the bull and its herd shifted to a grazing area. The third period of intensive movement was before midnight, when the whole herd galloped for about 500 metres to avoid one spotted hyaena, which did not pursue them.

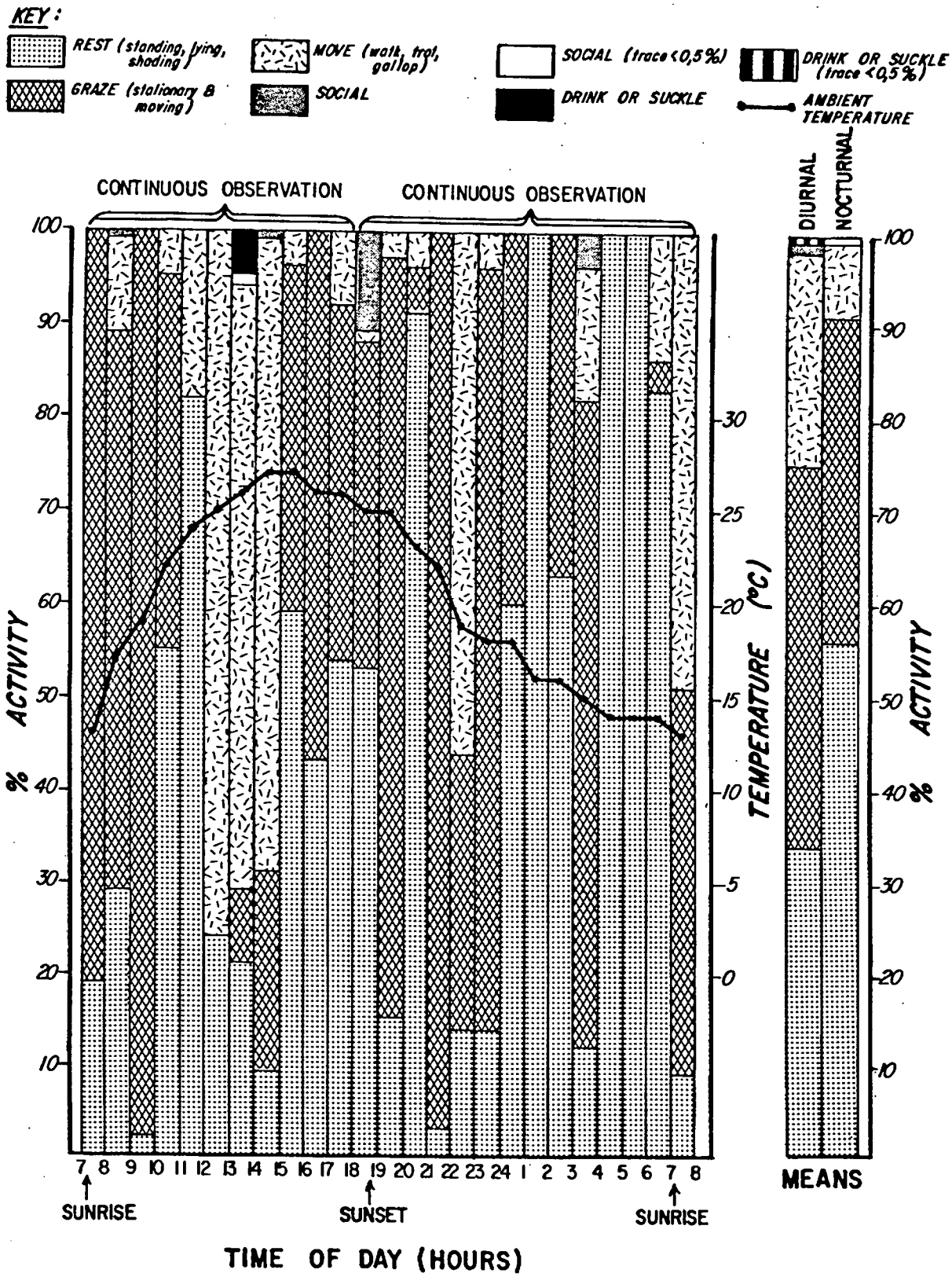

Fig. 4.7 : Diurnal and nocturnal activity of an adult, territorial bull wildebeest at Etosha, using the focal animal method. Ambient temperature is shown against the right-hand axis.

The bull displayed social behaviour five times : three times in the day towards cows in the herd, once intensively, shortly before sunset when a second bull was chased from the territory, and once in the early morning when the entire herd took part in a session of play. Water was drunk once, at midday, the period of actual drinking taking 100 seconds. Comparing the means for diurnal and nocturnal activity, it appeared that more resting occurred at night (56,2 % of total time) than in the day (35,5 %). There was slightly less grazing at night (35,5 %) than in the day (39,9 %). Movement at night (8,1 %) was noticeably less than in the day (23,4 %). The time spent in social encounters constituted 0,7 % of the total recorded. My estimates for the distance moved by the bull during the sampling were 6,4 km during daytime and 4,5 km at night. If the sample reflected 50 % of movement, which it was designed to do, then the daytime distance covered would be 12,8 km and the night-time distance 9,0 km. The vehicle's odometer could not always be used as a means of checking this, because on occasions the vehicle was stationary whilst the focal-animal moved back-and-forth.

4.3.5.4 Statistical Tests for Significant Differences in Activity Between Age-Sex Classes

(a) Analysis of Variance (ANOVA)

A two-way ANOVA with replication (Zar, 1974) was provided by a Univac computer, using unweighted means. The ANOVA was modelled so that each of the 13 detailed activity categories (Appendix 7) was a dependent variable input. Furthermore, the factor of age-sex class was compared against each activity, as was the factor of month. In addition, the interaction of age-sex and month was compared to each activity. Statistically significant differences were found in the resting and movement categories ($P < 0,05$), while highly significant differences existed on a monthly basis for the type of water drunk and for suckling ($P < 0,01$). However, in several cases the calculated F-value was less than 1, probably because the "error" (within cells) was too large. This invalidated the use of Fischer's test (Arkin and Colton, 1950). The ANOVA therefore indicated that significant differences existed between certain activities in regard to age-sex and month but did not specify the latter two factors. Because of this and because of the large "error" inherent in the ANOVA, I employed the Chi-square test.

(b) Chi-square Test

To test the null hypothesis (Zar, 1974), I entered the actual number of seconds recorded against an activity as the observed frequency for a particular age-sex class. The theoretical or expected frequency of this activity was computed from the mean of the observed number of seconds recorded for the age-sex classes being compared.

For example :

$$\text{Chi-square} = \sum_{i=1}^{n} \frac{(O_i - E_i)^2}{E_i}$$

where O_i = observed frequency

E_i = expected frequency

thus : if O_i = 1 000 seconds recorded against age-sex class A and

500 seconds recorded against age-sex class B

then : $E_i = \frac{1\,000 + 500}{2}$

$= 750$ seconds

The null hypothesis is that the frequencies of occurrence in the activity of age-sex classes A and B are equal. If the computed Chi-value exceeded the tabulated Chi-value at

a given fiducial level of probability, I rejected the null hypothesis and concluded that the activity of age-sex classes A and B differed significantly. For the purpose of my tests, I accepted 0,001 as the fiducial level of probability to indicate significant differences in activity.

Table 4.7 and Appendix 8 give the results of this analysis, based on a comparison between age-sex classes, of the total number of seconds spent during a year, in the various major activity categories. All comparisons were based on a corrected, equal sample size (n = 20 x 900-second samples per age class per day sampled). The conclusions made in Table 4.7 mostly support the findings on other free-ranging African ungulates (Leuthold, 1977; Sinclair, 1977) and are explained in the subsequent discussion (Section 4.3.6). One finding which is questionable, probably because of the small amounts of time recorded, was the significant difference in the amount of time spent in social encounters by adult cows and immature cows. It is unlikely that an adult cow is significantly less socially active than an immature cow.

4.3.6 Instantaneous Scans of Herds in Combination with Focal-Animal Studies

To compare the variation of activity in wildebeest herds as

Table 4.7 : Differences found between the amounts of time spent in four activity categories by the major age-sex classes of wildebeest at Etosha (1977-78)

Age-Sex Class Compared	Activity Compared	Conclusion made at P < 0,001
Adult bull : Adult cow	Resting	Bulls rest less than cows
	Grazing	Bulls graze less than cows
	Movement	Bulls move more than cows
	Social	Bulls are socially more active than cows
Immature bull : Immature cow (1 - 2 years of age)	Resting	Bulls rest less than cows
	Grazing	Bulls graze more than cows
	Movement	Bulls and cows move equally
	Social	Bulls are socially more active than cows
Adult bull : Immature bull	Resting	Adults rest more than immatures
	Grazing	Adults graze less than immatures
	Movement	Adults move more than immatures
	Social	Adults are socially more active than immatures
Adult cow : Immature cow	Resting	Adults rest less than immatures
	Grazing	Adults graze more than immatures
	Movement	Adults and immatures move equally
	Social	Adults are socially less active than immatures*

Table 4.7 (continued)

Age-Sex Class Compared	Activity Compared	Conclusion made at P < 0,001
Adults : Calves (< 1 year old)	Resting	Adults rest less than calves
	Grazing	Adults graze more than calves
	Movement	Adults move more than calves
	Social	Adults are socially more active than calves
Immatures : Calves	Resting	Immatures rest less than calves
	Grazing	Immatures graze more than calves
	Movement	Immatures move more than calves
	Social	Immatures and calves are socially equally active
Newborn bull calf : Newborn cow calf (< 1 week old)	Resting	Both sexes rest equally
	Grazing	Neither sex grazes
	Movement	Both sexes move equally
	Social	Both sexes are socially equally active

* See text for explanation

well as in the major age classes of bulls and cows, it was necessary to use data from both scan and focal studies. As in the case of the focal-animal study (Section 4.3.5), the volume of data obtained from scans made it necessary to limit discussion to a seasonal basis. Nocturnal scans of herds were relatively easier than nocturnal focal-animal studies, and so I was able to construct a reasonably complete model for the 24-hour activity cycle of wildebeest.

4.3.6.1 Seasonal and Yearly Diurnal Activity Patterns of Bull Herds and Mixed Herds

The activities of the two discrete herd types into which wildebeest congregate (Estes , 1966) are shown for three seasons and for the year in Fig. 4.8. The mixed herds at Etosha usually included an adult bull, adult cows, sub-adult bulls and cows aged 1 - 2 years, and calves of both sexes. Exclusively bull herds, the so-called "bachelors" (Estes, 1966), comprised all ages of adults, as well as a small percentage of bulls approaching their second year, which had been driven from the mixed herds. Lone, territorial bulls were not considered for this comparison. Instead, I have discussed them in conjunction with the other bull age classes (Section 4.3.6.2).

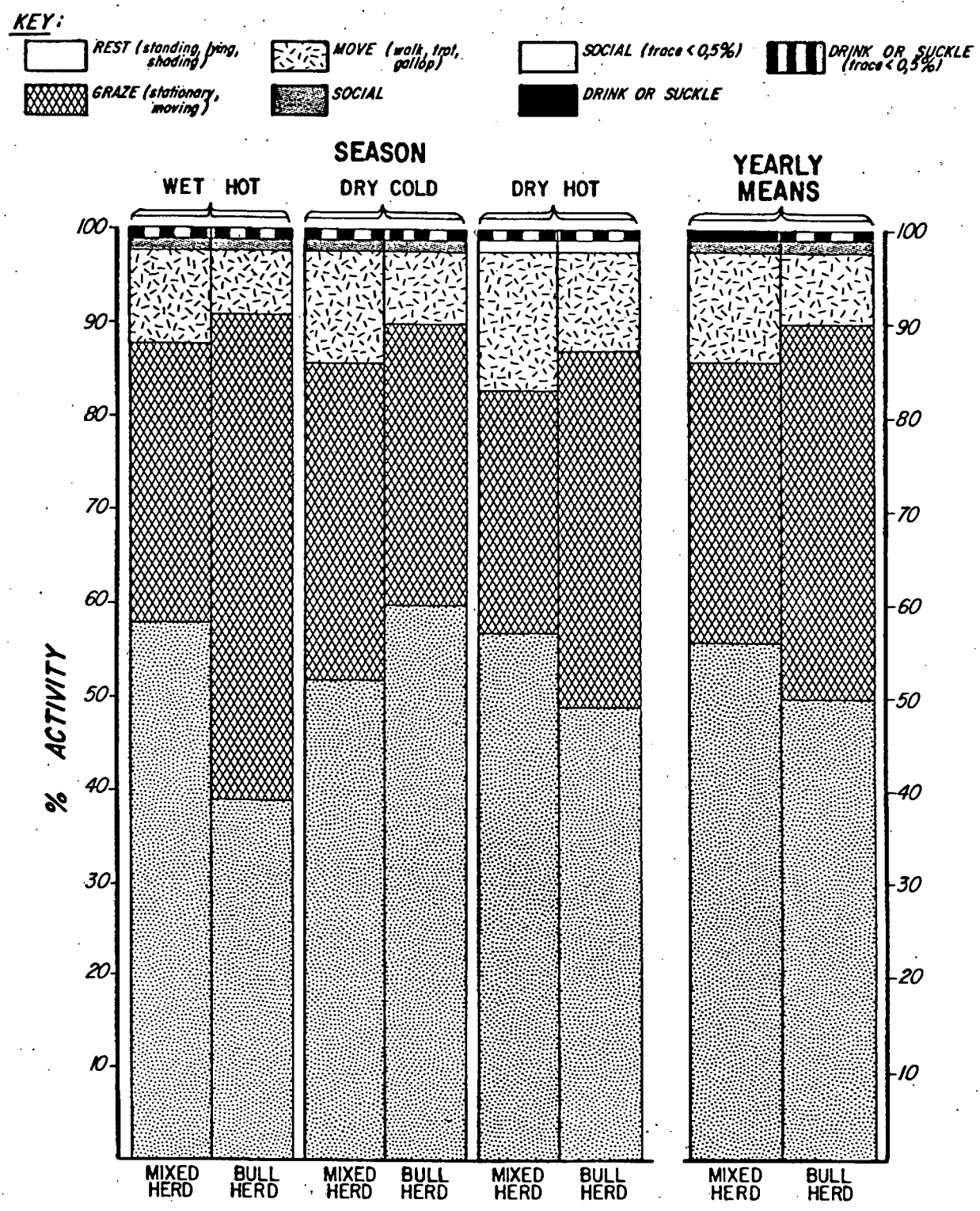

Fig. 4.8 : Seasonal diurnal activity patterns of wildebeest herds at Etosha, using the instantaneous scan method.

(a) Wet, Hot Season (January to April)

The higher rate of resting in mixed herds (58 %) was due to the presence of newborn calves, which were largely inactive. Mixed herds or "nursery" herds (Estes, 1966) usually occupied the best grazing areas. Consequently they required less foraging effort and this was reflected in the lower amount of time allocated to grazing (30 %). The higher rate of movement in mixed herds (10 %) was caused by the adult bulls in rut which patrolled the herds frequently. In contrast to this pattern, the bull herds were relegated to inferior grazing areas. They were forced to decrease resting (39 %) and increase their rate of foraging (52 %). Not being actively involved in the rut, they displayed no territoriality (Estes, 1968) and so moved less (7 %). Both the herd types displayed social behaviour at a 1 % level. In mixed herds, the rutting bull was responsible for most of this, but the frequency of his social encounters in relation to those of the total herd were obviously reduced in the overall results, by the scan method. Social encounters in bull herds were limited to non-aggressive, playful sessions. Both herd types drank seasonal water from temporary rainwater pools (< 0,5 %).

(b) Dry, Cold Season (May to August)

In this period the mixed herds decreased their resting rates as calves grazed more effectively and the herd bulls ceased intensive patrolling. There was an increase in grazing and movement, although marginal, as food and water became less available. The bull herds however, rested and grazed at noticeably higher rates than in the preceding season. I ascribed this to the lower level of physiological stress to which they were subjected when account is taken of lactation and growth of calves and sub-adults in the mixed herds. Bull herds also moved less than mixed herds at this time. Social encounters in both herd types were at a 1 % level of frequency and with the drying of rainwater pools, the herds began drinking perennial water.

(c) Dry, Hot Season (September to December)

The dry, hot season at Etosha was relatively more stressful in terms of both food and water. Mixed herds were nevertheless able to rest at a high rate and spent less time grazing than bull herds. However, they moved more. I was able to offer the following explanation for such a strategy, from my observations. During this period the activity patterns of wildebeest were centred around the

need to drink water every day. I noticed that bull herds were mostly in the vicinity of perennial waterholes and consequently they were in trampled areas of relatively poor grazing. They needed less movement than mixed herds however, to obtain water. The mixed herds occupied better grazing areas which required less foraging time. These areas were farther from water and they paid for the privilege of better grazing by having to move greater distances to drink. Similar activity patterns exist in mixed and bull herds of buffalo (Sinclair, 1977). Social encounters were less than 0,5 % in both herd types. The reduced level was in keeping with an absence of sexual activity and less evident territories in wildebeest at this time of year.

(d) Yearly Means of Activity in Wildebeest Herds

Fig. 4.8 also summarises the findings on activity over three seasons, expressed as a yearly mean for mixed herds and bull herds. From this it was evident that mixed herds rested more, moved more and spent less time foraging than bull herds. Both herd types displayed social behaviour at equal levels. There was a higher level of drinking in mixed herds. This was caused by the suckling of calves, which was included in this category of activity.

4.3.6.2 Seasonal Diurnal Activity Patterns for the Major Age Classes of Bulls

In Fig. 4.9 bulls have been divided into five age and social classes. The scans provided information about bachelor and adult mixed herd bulls. To incorporate lone, adult territorial bulls, I referred to focal-animal data, since scanning was not carried out on single wildebeest. I also used focal-animal data in the case of sub-adults (1 - 2 years old) and calves (less than one year old), because scans did not differentiate between the sexes for these age classes.

(a) Wet, Hot Season (January to April)

Very young bulls, being newborn to two months old, rested as much as 74 % of the time. The independent, growing sub-adults could only afford to rest for 21 % of the day. Bachelor bulls, being two years and older, and therefore full-grown, rested nearly twice as much as sub-adults (40 %). Bulls holding mixed herds were rutting at this time, but presumably they were in prime condition and so could afford a fairly high resting frequency (47 %). In contrast, lone bulls which had not succeeded in keeping a breeding herd in their territory, rested less (37 %). The rates of grazing showed that young bulls were dependent

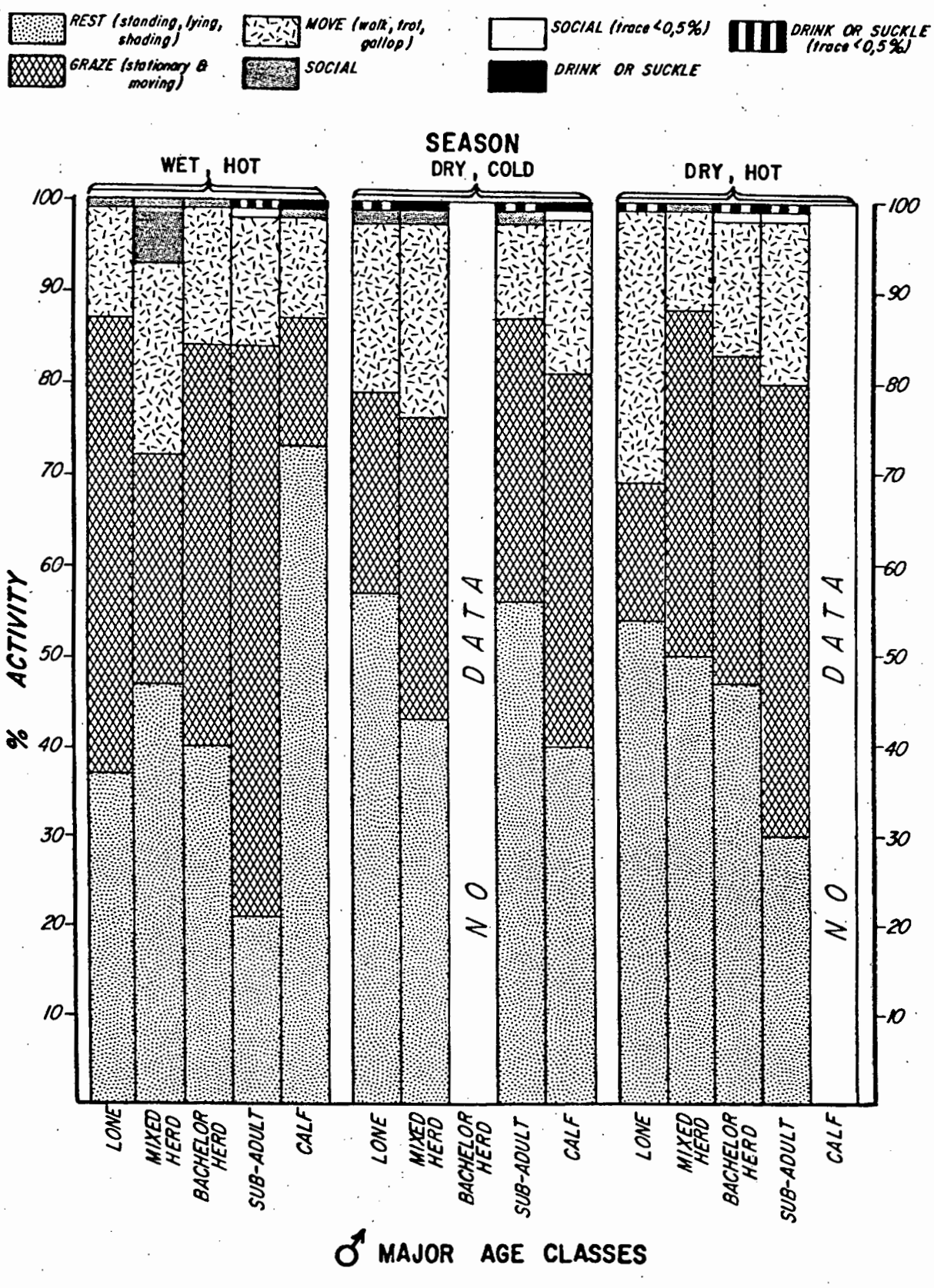

Fig. 4.9 : Seasonal diurnal activity patterns for the major age classes of bull wildebeest at Etosha, using the instantaneous scan and focal animal methods.

on milk for the major part of their diet and only grazed for 14 % of the time. Sub-adult bulls had the highest grazing frequency recorded for all age-sex classes of wildebeest, namely 63 %. Lone bulls, having no herd to control, were able to spend 50 % of their day grazing. In contrast, rutting herd bulls grazed only half as much as their single counterparts (25 %). Movement was a very important part of the herd bulls' day. They spent 21 % of their time patrolling the outskirts of the herd. This served two purposes. It kept away intruding bulls and prevented the herd escaping from the bull's selected territory. Bulls in the remaining social status and age classes all spent less time in movement (11 % - 15 %). Predictably the level of social behaviour was the highest in bulls attending mixed herds during the rut (7 % of the total time recorded). All other bulls spent 1 % or less of their day in social encounters.

(b) Dry, Cold Season (May to August)

No data on a complete diurnal scan could be obtained in the case of bachelor bulls. The increasing independence of bull calves led to a drop in their inactivity and they grazed nearly as much as they rested (40 % - 41 %). The adult bulls attending mixed herds completed the rut in May, but because of the physiological stress it imposed,

they increased their grazing frequency at the expense of resting (33 % and 43 % respectively). Lone bulls were not subjected to the same stress and consequently could afford to rest for 57 % of their day. They had probably also accumulated sufficient reserves of fat from the good grazing available in the preceding season, so that they needed only to graze at a reduced frequency of 22 %. Sub-adult bulls showed a sharp increase in resting and a reduced level of grazing, possibly to compensate for the very high level of grazing activity during the wet, hot season. Their greatly improved condition due to the nutritive value of grass in that season probably made more resting time available to them. Reduced availability of water accounted for most of the movement of all groups of bulls. In addition, the bulls in mixed herds and the lone bulls still patrolled their territories, accounting for the higher rate of movement they showed in relation to the sub-adults and calves. Social encounters by mixed herd bulls, lone bulls and sub-adults were at a similar level (2 %). This reflected the ending of the rut. Sub-adult bulls were engaged more noticeably in social encounters with cows who began to drive them out of the mixed herds. Calves showed only a trace (< 0,5 %) of social behaviour in this period.

(c) Dry, Hot Season (September to December)

I was unable to collect complete diurnal activity data for bull calves during this season. The two environmental factors affecting all wildebeest in the dry, hot season at Etosha were reduced quantity and quality of grass and reduced availability of water to drink. This in turn affected their activity patterns. Bulls in mixed herds occupied the best grazing areas and did not have to search for food as much as the bachelor herds. This was shown in the differences between their resting and movement. The time they spent grazing was, however, very much the same (36 - 38 %). Lone bulls had an interesting activity pattern at this stage. They rested more than any other bulls (54 %) and grazed surprisingly little (15 %). Their movement was largely responsible for this and was caused by the long distance they were forced to move to drink. My observations showed that lone bulls occupied territories which were further from water than any other wildebeest. One bull was located 15 kilometres from the nearest waterhole and this meant that to drink and return to his territory would require a minimum movement of 30 kilometres, probably every day. Sub-adults rested considerably less (30 %) than they grazed (50 %). Their eviction from the mixed herds had mostly taken place by then and they were becoming affiliated to bachelor herds. Consequently their grazing

areas were inferior (Estes, 1966) and they also had to contend with growth. Their increased foraging time was linked with increased movement. Only herd bulls behaved socially to any noticeable extent, while a trace of social encounters was recorded in bachelor bulls and sub-adult bulls. No social behaviour was seen in the lone bulls observed during this period.

4.3.6.3 Seasonal Diurnal Activity Patterns for the Major Age Classes of Cows

Adult cows (more than two years old) were compared against sub-adult cows (1 - 2 years old) and cow calves (< 1 year). For the adults I used instantaneous scan data and for the two immature classes focal-animal data was required, because scans did not distinguish between sexes of immature wildebeest. The results are given in Fig. 4.10.

(a) Wet, Hot Season (January to April)

Similar to young bull calves (Section 4.3.6.2), the cow calves rested 79 % of the day. They grazed 14 % and moved only 5 % of the time, relying mostly on milk during the first two months of life. In contrast, the sub-adult cows, which were one year older rested for only 29 % of the day, with 53 % allocated to grazing and 16 % to

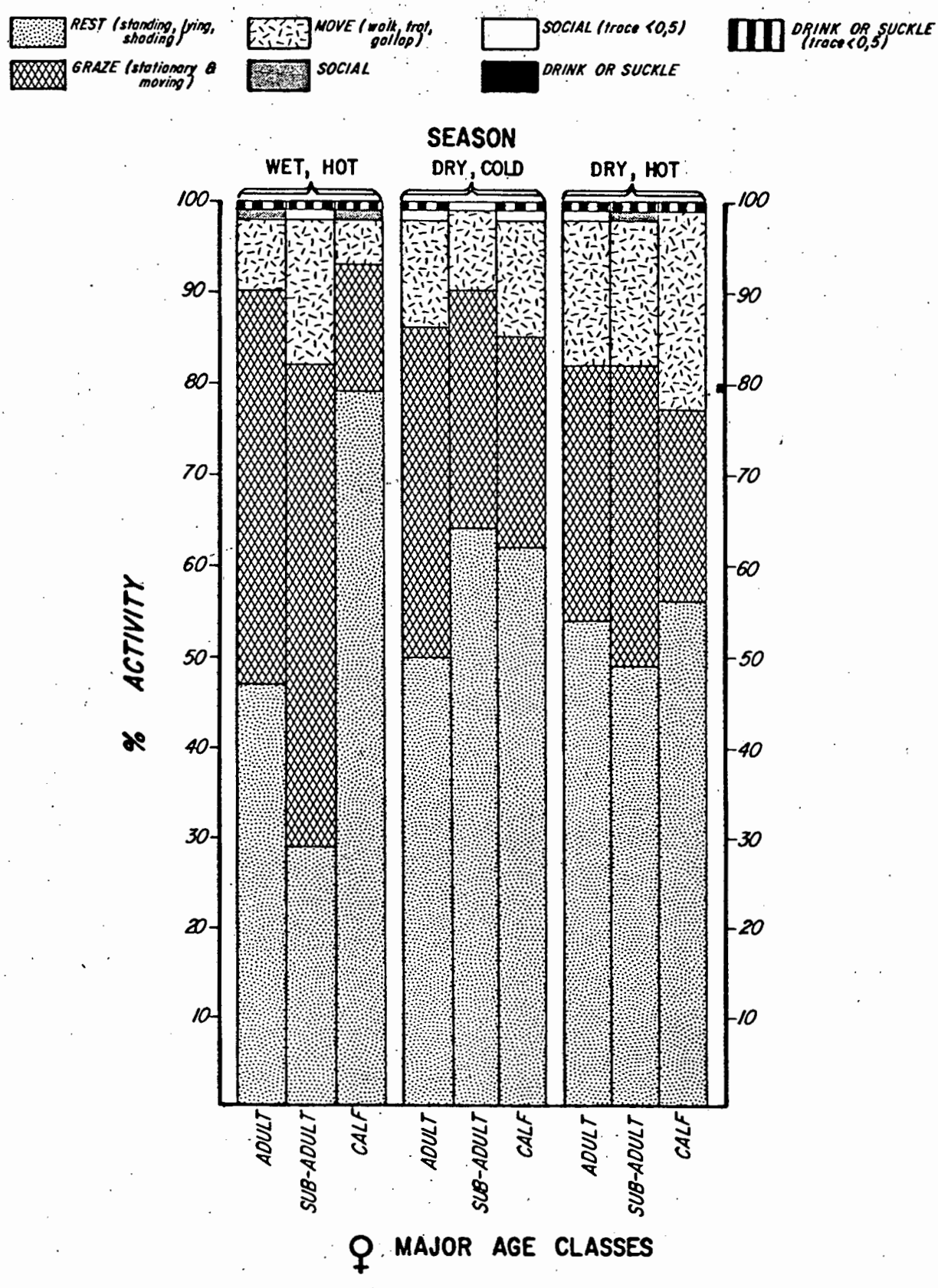

Fig. 4.10 : Seasonal activity patterns for the major age classes of cow wildebeest at Etosha, using the instantaneous scan and focal animal methods.

movement. This was in keeping with their stage of growth, but was not as pronounced as in the case of sub-adult bulls (Section 4.3.6.2). About 90 % of the adult cows were either pregnant or lactating at this time (Section 12.3), and consequently they spent almost as much time grazing (43 %) as resting (47 %). They moved relatively little (8 %) compared to the sub-adult cows or the bulls (Section 4.3.6.2). Social activity in all age classes of cows was 1 % and lower.

(b) Dry, Cold Season (May to August)

Cow calves maintained a high level of resting (62 %) and grazed 23 % of the day. This was far less than bull calves, which spent 41 % of their day grazing (Section 4.3.6.2) and may have been related to a difference in their respective rates of independence. Sub-adult cows showed much the same frequencies of resting and grazing as the cow calves. It is worth noting that, similar to the sub-adult bulls (Section 4.3.6.2), the sub-adult cows also increased the time spent resting considerably in relation to the preceding season, but not by the same magnitude. Adult cows rested less (50 %) than the younger cows and grazed more (36 %), probably because they still suckled calves, although at a much reduced rate. All age-classes of cows had similar rates of movement,

which was generally less than in the case of bulls at this time (Section 4.3.6.2).

(c) Dry, Hot Season (September to December)

There were no spectacular differences in any of the activities of the age-classes of cows. This is in direct contrast to what was recorded for the bulls (Section 4.3.6.2) and can be explained by the heterogeneous social levels existing in bulls (Estes, 1968). Adult cows increased their resting compared to the preceding season to 54 % and grazed less (28 %), due to increasing independence in their calves. The sub-adult cows, then approaching two years of age, rested slightly less than the adults, with an appropriate increase in grazing time. Their rate of movement was the same as the adult cows. Cow calves continued with a lower frequency of grazing (21 %) than the adults and sub-adults and accordingly rested and moved more. Social behaviour was not recorded in cow calves at this time, while sub-adult and adult cows behaved socially at a 1 % or lower level.

4.3.6.4 Seasonal Diurnal and Nocturnal Activity Patterns of Bull Herds and Mixed Herds

Instantaneous scans were used exclusively to obtain these

data. Bull herds were easier to follow during the day and more so at night than mixed herds. I found that bulls could be observed at closer range than mixed herds which were noticeably more sensitive to my vehicle's presence, especially at night.

The results for four days and four nights of scanning herds are presented on an hourly basis of 24 hours each in Figs.4.11 to 4.14. Ambient temperatures are given for each hour. Results of the nocturnal scans only, have been summarised on a seasonal basis and are shown in Fig. 4.15. In this figure a fifth nocturnal scan on a bull herd has been included under the dry, hot season. This particular herd was located nearby the mixed herd I was scanning and it was possible to observe their activity throughout the night but not by the standard scanning procedure. They are included as a set of casual observations and have not been taken into account for the calculation of seasonal means in Fig. 4.15. Finally, I have compared the gross diurnal activity of all age-sex classes of wildebeest during one year (n = 20 complete scans) to their nocturnal activity (n = 4 complete scans) (refer to Fig. 4.16). The greater number of diurnal observations obviously makes the estimate of activity more reliable than that for nocturnal observations. However, no quantitative data on either diurnal or nocturnal activity

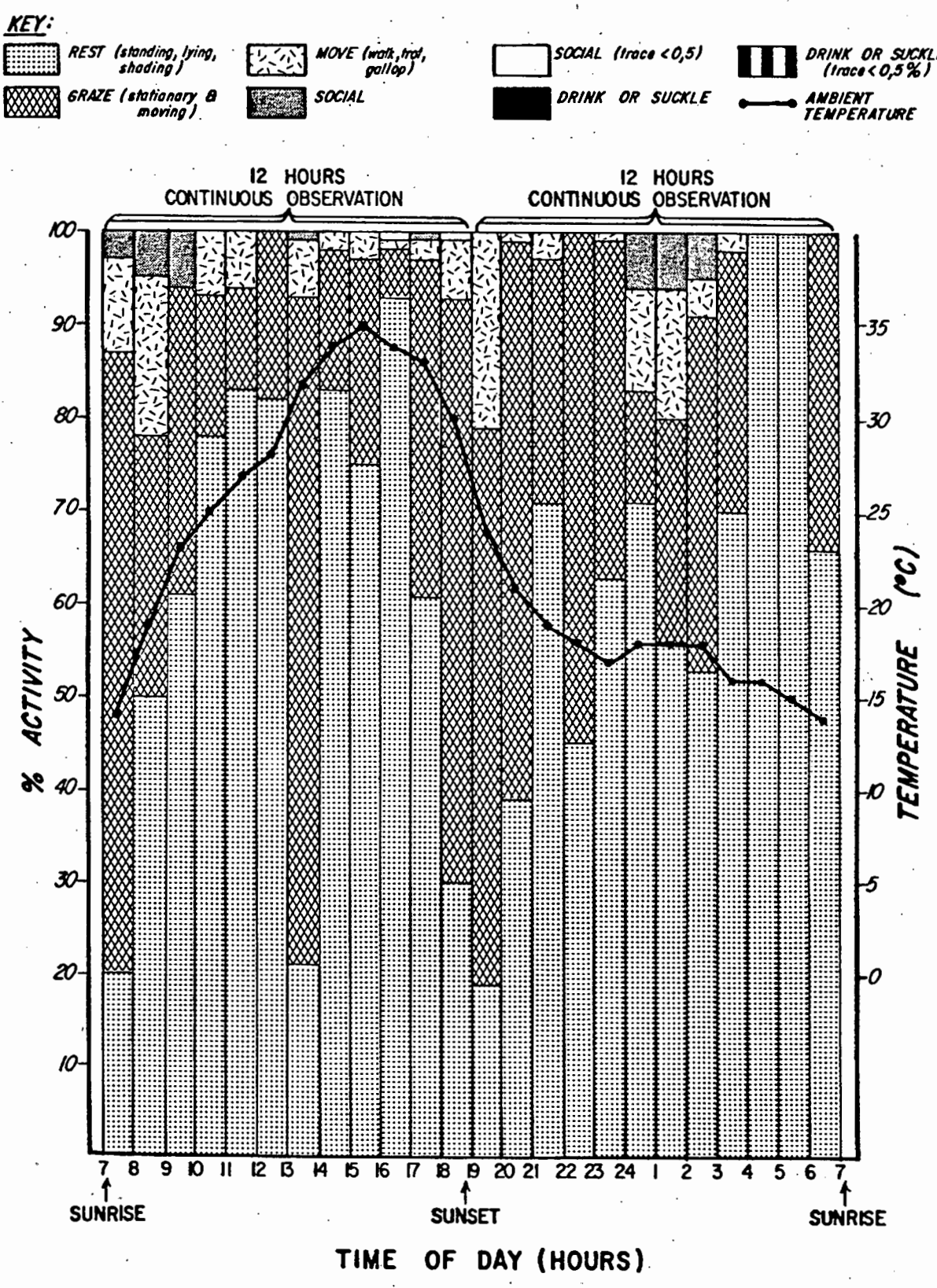

Fig. 4.11 : Diurnal and nocturnal activity of a herd of bull wildebeest at Etosha during the wet, hot season, using the instantaneous scan method.

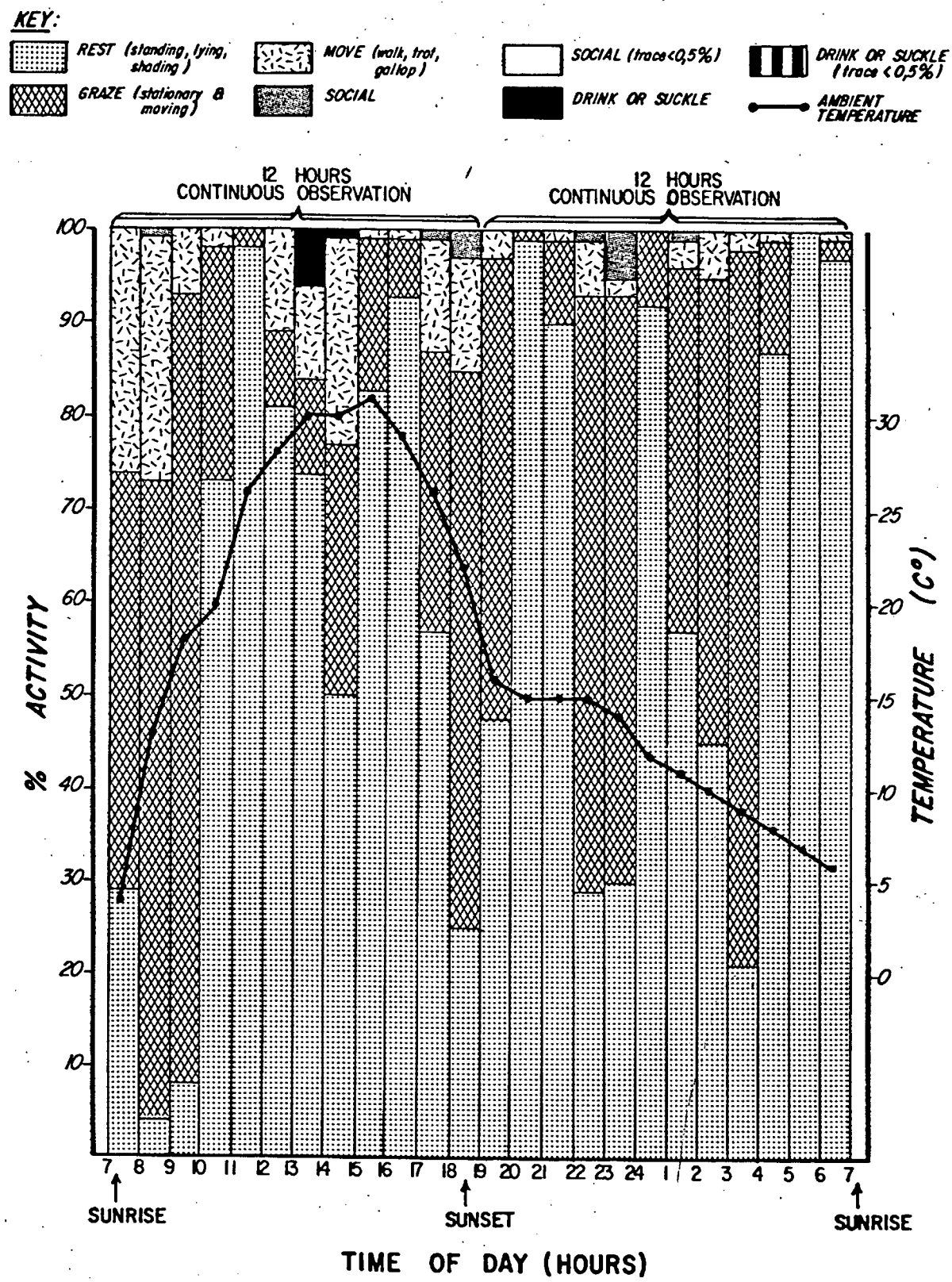

Fig. 4.12 : Diurnal and nocturnal activity of a herd of bull wildebeest at Etosha during the dry, cold season, using the instantaneous scan method.

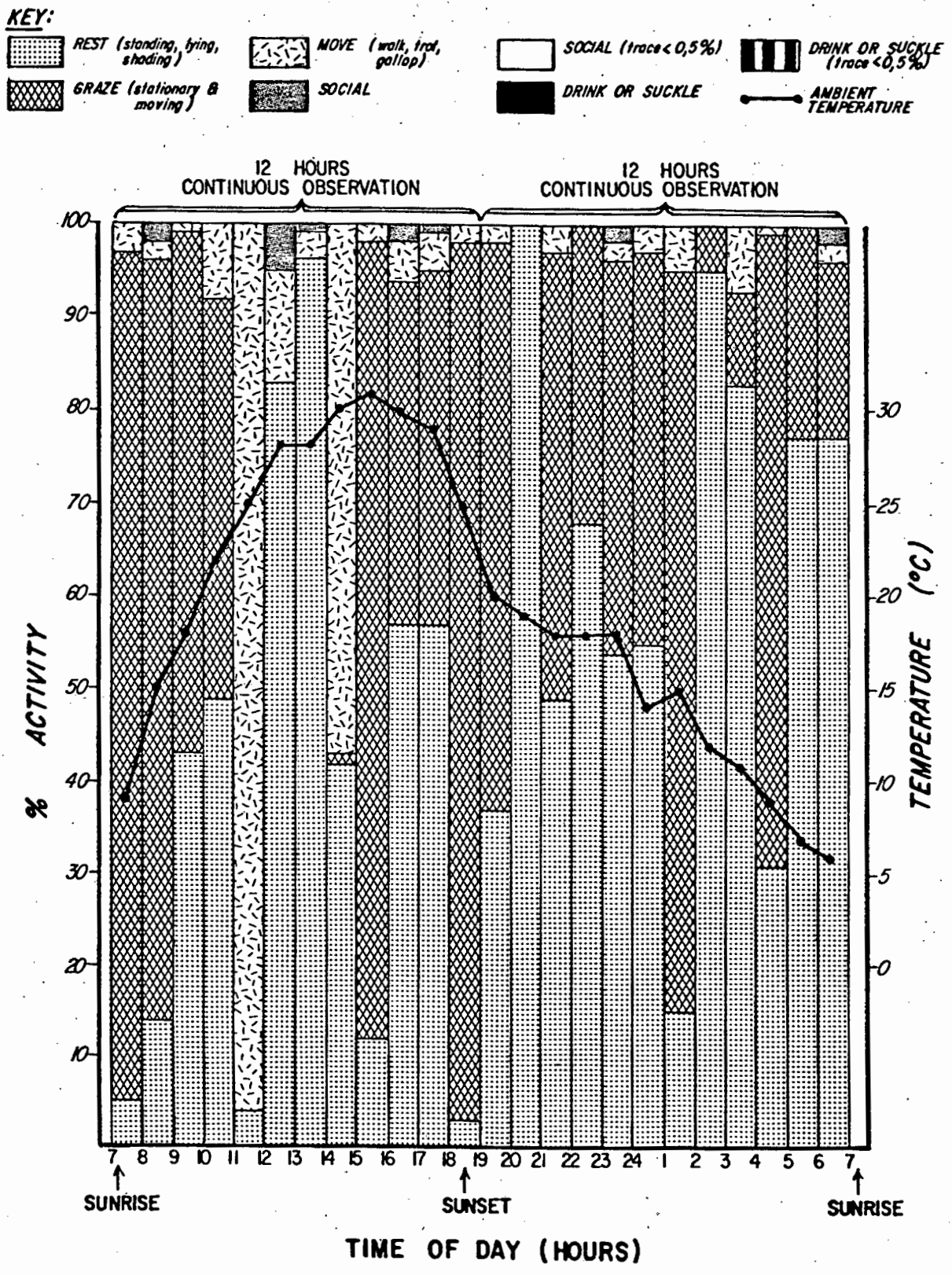

Fig. 4.13 : Diurnal and nocturnal activity of a mixed herd of wildebeest at Etosha during the dry, cold season, using the instantaneous scan method.

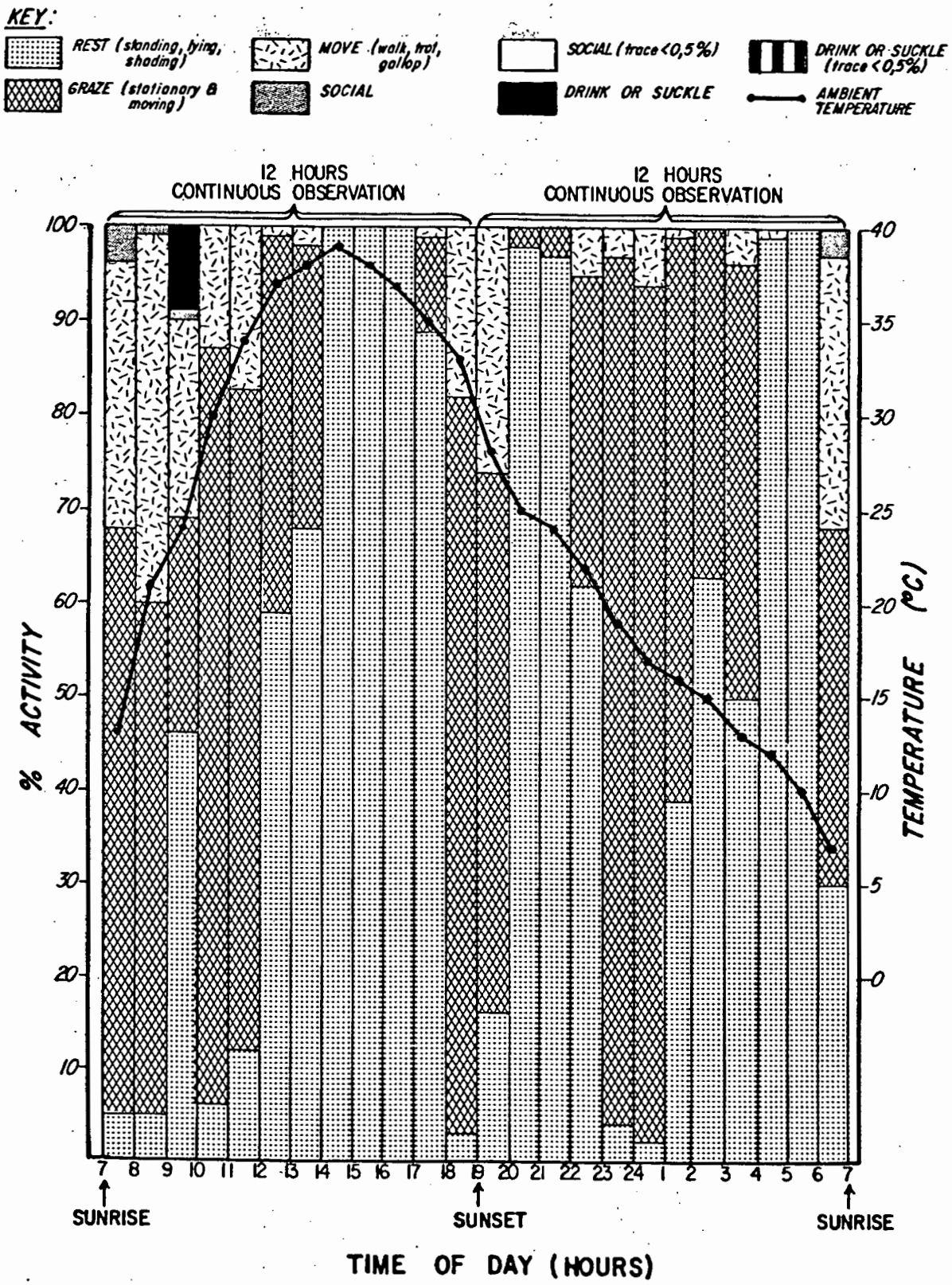

Fig. 4.14 : Diurnal and nocturnal activity of a mixed herd of wildebeest at Etosha during the dry, hot season, using the instantaneous scan method.

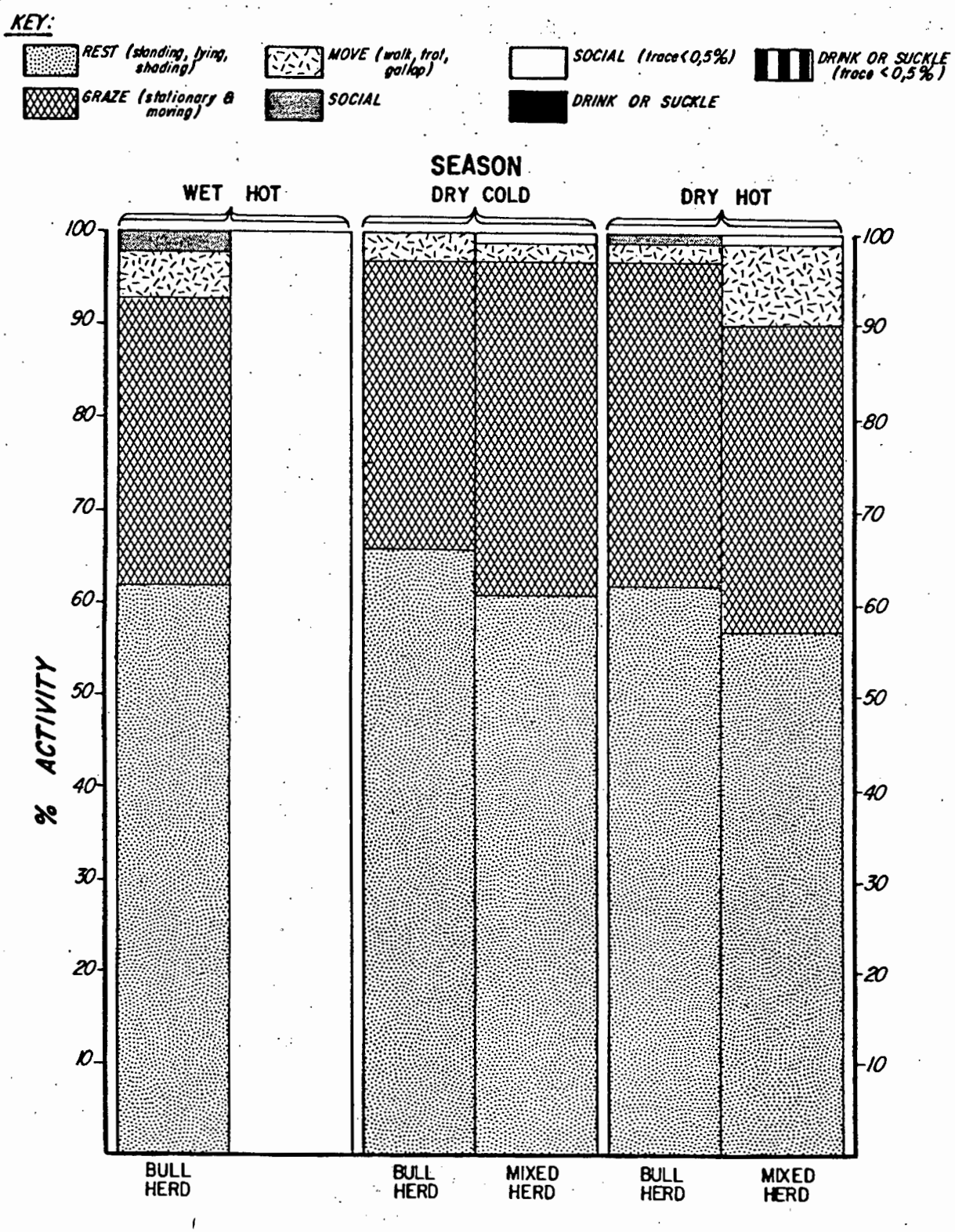

Fig. 4.15 : Seasonal nocturnal activity of bull herds and mixed herds of wildebeest at Etosha, using the instantaneous scan method.

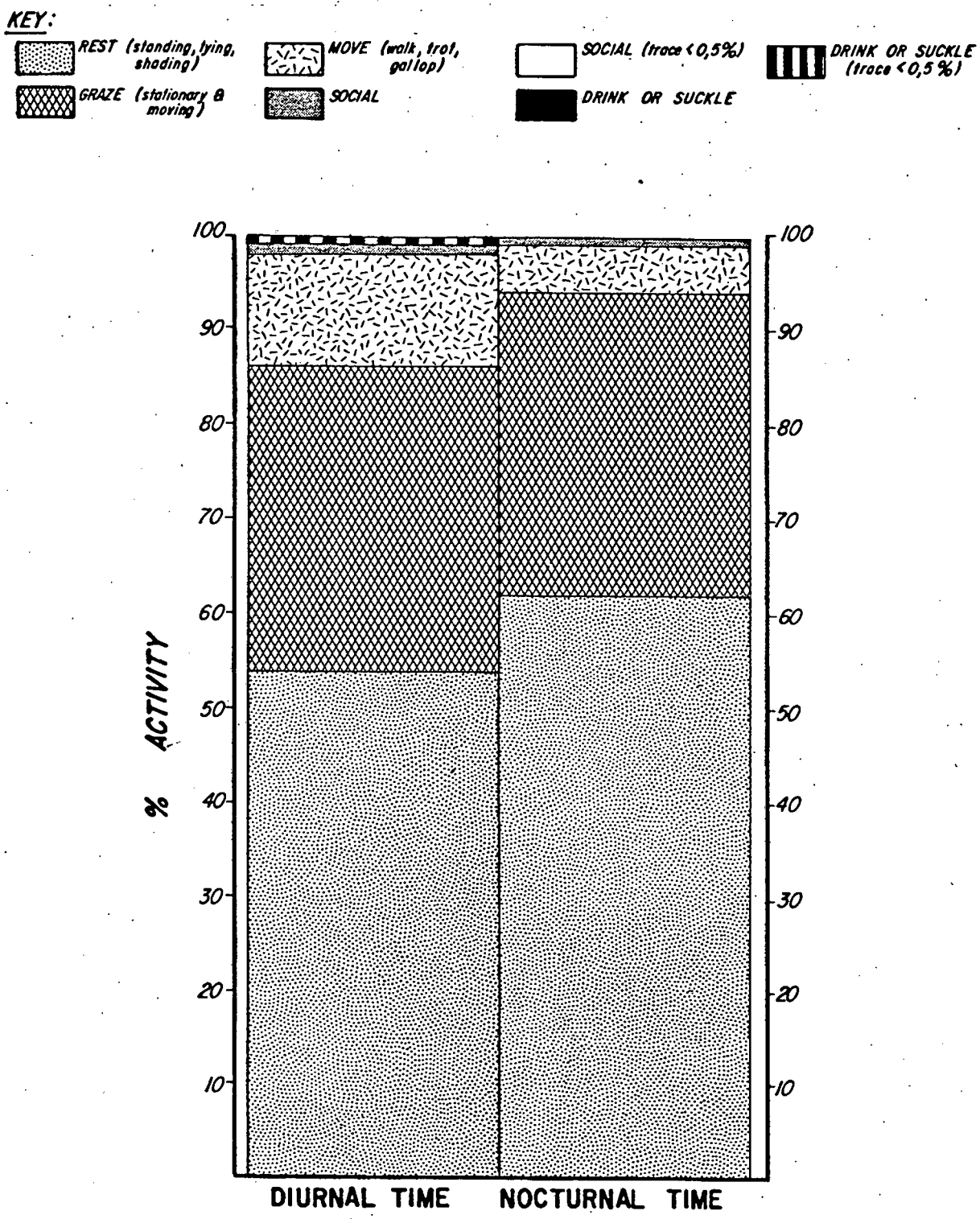

Fig. 4.16 : Comparison of diurnal and nocturnal activity in bull herds and mixed herds of wildebeest at Etosha, using the instantaneous scan method.

patterns of free-ranging wildebeest have been available previously. The present estimates may be improved by further research.

(a) Wet, Hot Season (January to April)

Three resting peaks (> 75 %) occurred during a period of 24 hours in the bull herd studied. Two of these were during the day and one in the early morning hours (Fig. 4.11). The two daytime peaks of resting were probably associated with high ambient temperatures and a linear relationship was found to exist (Section 4.3.5.1). However, it was apparent that on average, the bulls rested virtually the same amount of time during the day ($\bar{x}$ = 61,5 %, n = 12 hours) as they did at night ($\bar{x}$ = 62,7 %, n = 12 hours). Similarly, there were three peaks of grazing : one just after sunrise, one at midday and one the hour after sunset. Again, there was very little difference between the average time spent grazing (32,4 % in the day and 31,1 % at night). Noticeable movement (> 10 %) took place after sunrise, after sunset, and at midnight. The movements at sunrise and sunset were linked to intensive grazing. Average daytime movement was 4,9 % and at night 4,8 %. Social behaviour was prominent at sunrise and again at midnight when most of the bulls engaged in a playful session. Although the recorded time

(50 % of 24 hours) showed no drinking, rain water was drunk once from a temporary pool, towards midday. This took place during non-recorded time.

(b) Dry, Cold Season (May to August)

In this period, I was able to obtain complete diurnal and nocturnal data for a bull herd and a mixed herd. The bull herd had five peaks of resting. Two occurred in the day (mid-morning and mid-afternoon) and three at night (after sunset, at midnight, and before sunrise). Daily resting average was 56,2 %, which was lower than the night's average of 66,5 %. There were four peaks of grazing, namely, at sunrise, at sunset, towards midnight, and during the early morning hours. Little difference existed between the day grazing ($\bar{x}$ = 32,2 %) and the night grazing ($\bar{x}$ = 31,1 %). Three periods of noticeable movement (> 10 %) occurred. All were in daytime. Two were linked to the grazing peaks at sunrise and at sunset, and one was linked to drinking in the early afternoon. Thus, much more movement occurred in the day (10,8 %) than at night (2,0 %). This decreased the day's resting time. There were two periods of noticeable social behaviour : one at sunset and again at midnight.

The mixed herd showed four resting peaks, only one of which

occurred in the day, during early afternoon. The three night peaks of resting were shortly after sunset, in the early morning and shortly before sunrise. The daily resting average of 38,9 % was much less than the nightly average of 61,7 %. There were four peaks of grazing : at sunrise, mid-afternoon, at sunset, and shortly after midnight. On average, 44,1 % of the day was spent grazing, compared to 35,8 % at night. The most noticeable difference between day and night activity was the time spent in movement (day $\bar{x}$ = 16,2 %, night $\bar{x}$ = 2,1 %). The only significant movement was the trek to and from perennial water, which was drunk during non-recorded time at midday. The greatest amount of social activity also took place at the drinking place, where herds mingled. Thus, the two herd types showed certain similarities in their diurnal-nocturnal activity patterns at this time of the year. Both rested more at night and moved more in the day, the mixed herd showing great differences in this respect.

(c) Dry, Hot Season (September to December)

The mixed herds I observed had one daytime resting peak, which lasted most of the afternoon, and two nighttime resting peaks, after sunset and again before sunrise. Average resting time in the day (49,4 %) was less than at

night (55,1 %). Four periods of intensive grazing occurred : at sunrise, during mid-morning, at sunset, and at midnight. The grazing averages for day and night were, however, exactly the same (37,6 %). There were two periods of noticeable movement (> 20 %), namely, a sunrise peak of movement which was linked to the return journey of about 4 km to drink water at mid-morning, and movement to graze at sunset. Social behaviour was only recorded at sunrise, when the herd became active, and at the waterhole.

(d) Differences in 24-Hour Activity Patterns Caused by Season

Figs. 4.11 to 4.14 suggest the following tendencies in activity of wildebeest. The wet, hot season had daytime temperatures which reached 35 ^{o}C and these high ambient temperatures probably initiated the two major daytime periods of inactivity. Grazing was therefore limited to intensive periods of short duration. To compensate for this at night, the wildebeest showed a more even rate of grazing and consequently of resting. This continued until the volume of food intake required a lengthy period of resting and rumination, which took place during the last few hours of darkness. Temperatures were also at their lowest in this period and wildebeest conserved energy by lying down to rest. Intensive, heat-producing movement

was limited to the cooler times of day. The cold, dry season had lower ambient temperatures, allowing greater movement in the day. However, as temperature increased to a mid-afternoon maximum of 31,0 ^{O}C, the heat load was sufficient to cause one to two peaks of resting in wildebeest. Impinging on these peaks of inactivity was the strategy adopted by wildebeest to drink water at a time when predation was less likely (Section 4.3.5.1). Milder day temperatures also permitted grazing to take place at a more even rate than in the preceding season. As a result, the night's grazing-resting ratio was less distorted than in the hot, wet season. Movement was also more evenly distributed at night. The hot, dry season was the period of greatest environmental stress for wildebeest at Etosha. Daytime temperature reached a maximum of 39 ^{O}C by mid-afternoon, effectively dividing the day into two activity regimes. Inactivity was essential during the heat of afternoon, leaving only the cooler morning for grazing. This resulted in very clear, alternating bouts of grazing-resting-grazing from sunset to sunrise. Movement was similarly restricted by high temperatures to the coolest times of day. My contention therefore is that environmental temperature was a prime factor in determining the diurnal and nocturnal activity patterns of wildebeest at Etosha. Increase in temperature was directly related to their rate of inactivity during the

day as I have demonstrated in Section 4.3.5.1. It appears that temperature and photoperiod are the pivotal factors which determine to a large extent the remainder of the 24-hour activity cycle. Moreover, seasonal variations in this activity cycle seem to be directly linked to changes in the temperature regime.

(e) Comparison of Diurnal and Nocturnal Activity

Fig. 4.16 compares the mean diurnal and nocturnal activities of wildebeest. The data on nocturnal activity was limited to full moon periods and this may have affected activity compared to moonless nights (Leuthold, 1977). Nevertheless, differences can be expected in the diurnal-nocturnal activity of ungulates as shown by buffalo during 96 hours of consecutive observation during a full-moon period (Sinclair, 1977). In the case of Etosha's wildebeest, it appeared that food intake and social behaviour were the two constants during the day and night. Ruminants need to feed at relatively short intervals "to keep the system going" (Leuthold, 1977) and it is therefore not surprising that wildebeest foraged the same amount of time in the day and night. This occupied exactly 32 % of each period. Social behaviour was at a 1 % level in the day as well as the night.

The differences in diurnal and nocturnal activity were found in resting, movement and drinking of water. They all may have revolved around predator evasion. In this context, it was apparent that wildebeest very seldom drank at night from perennial waterholes at Etosha. This covered a period of about eight months of the year, because they obviously had freer access at night to numerous rainwater pools which formed during the wet, hot season. I obtained no records of nighttime drinking by wildebeest at permanent waterholes in five years of fieldwork at Etosha, although Du Preez and Grobler (1977) recorded wildebeest drinking there at night. During the present study it was evident that the majority of movement took place in the day when wildebeest went to drink water. This occurred at the expense of resting. Daytime movement to waterholes lessened the chance of predation, just as nighttime movement of any kind increased the likelihood of an ambush by lions. Since previous work on ungulates indicates a decrease in active movement during moonless nights (Walther, 1973) it is probable that my nocturnal observations on wildebeest at full moon showed the maximum activity which occurred. Further research on their nocturnal activity patterns is certainly necessary.

A major determinant of wildebeest activity patterns was

probably the diurnal photoperiod, since marked changes from inactivity to activity accompanied the changes in light intensity at dawn and dusk. Jarman and Jarman (1973) and Walther (1973) considered photoperiod to be a proximate cause of the basic diurnal-nocturnal activity patterns in impala and Thompson's gazelle respectively. Photoperiod and high ambient temperature (the latter has been discussed in paragraph (d) of this Section) are crucial factors in determining wildebeest activity.

4.3.7 The Synchrony Within Herds

Wildebeest were highly synchronised in their behaviour and an entire herd changed from one state to another within a few minutes. During diurnal and nocturnal scans of herds (Section 4.3.6.4), I was able to record this synchrony. To illustrate it, the active periods have been related to inactive periods and expressed as a proportion in Fig. 4.17. Three major periods of activity and inactivity are shown and the rapid change from one to another demonstrates the well-developed herd synchrony in wildebeest.

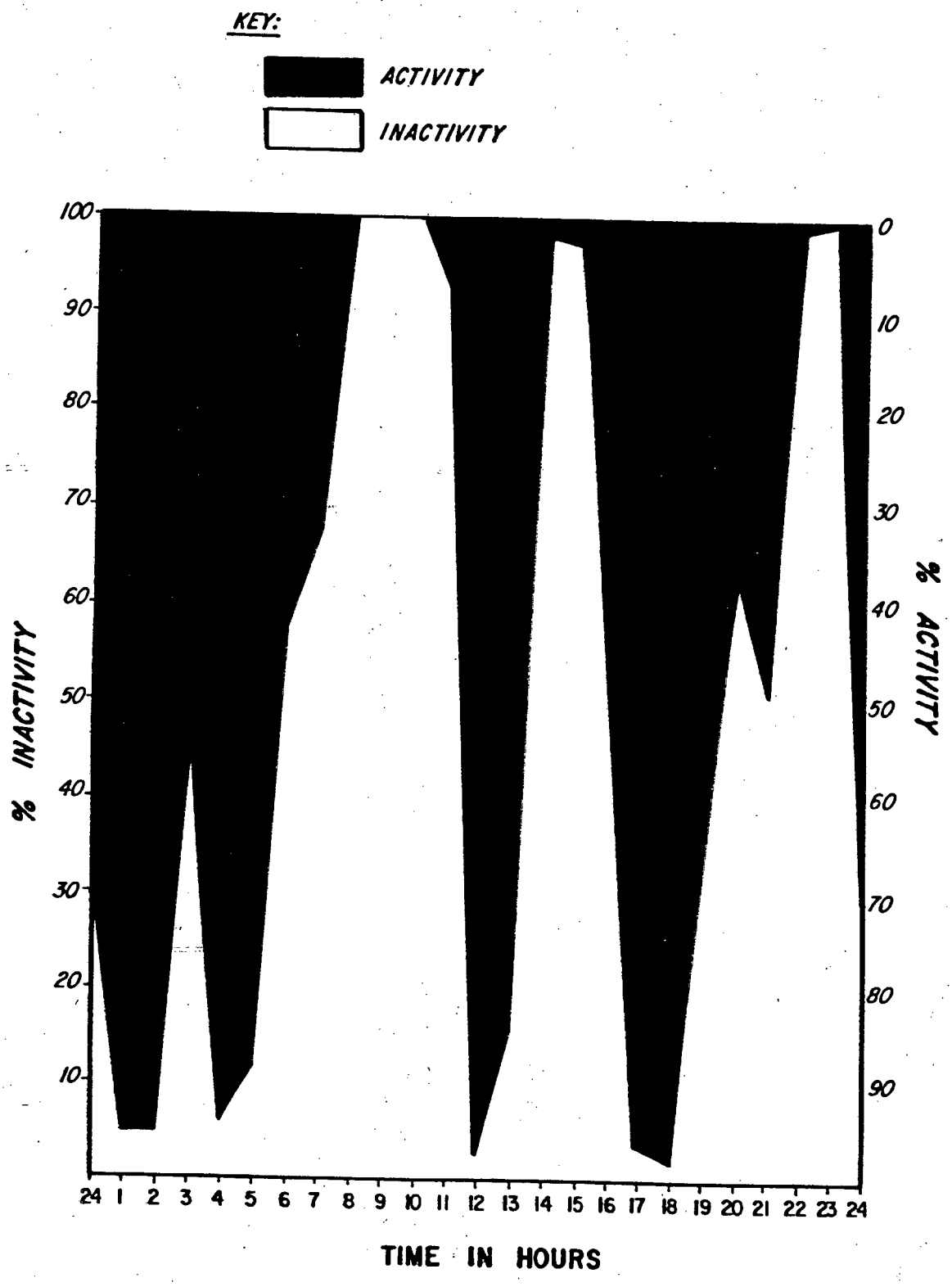

Fig. 4.17 : Proportion of activity to inactivity in a wildebeest herd at Etosha, measured on 10 observations per hour for 24 hours. The distinct peaks and troughs demonstrate the synchrony within a herd.

4.4 SUMMARY AND HYPOTHESIS

4.4.1 Summary

4.4.1.1

To quantitatively evaluate the diurnal and nocturnal patterns of activity in wildebeest at Etosha over a period of one year, focal-animal and instantaneous scan methods were successfully used. For the focal-animal study, a total of 263 hours of activity was recorded by stopwatch, entailing 43 days and one night of observation. Instantaneous scans covered 20 days and four nights, involving 66 690 classifications of activity in herds. Data were analysed with the aid of a computer. Comparison of the two methods showed no statistical difference in the results, on a seasonal or monthly basis. The overall results for the methods, during one year, were in close agreement.

4.4.1.2

The wildebeest population at Etosha spent about 53 % of its total time resting. Approximately 33 % was devoted to grazing and 12 % to movement. Overt social behaviour occupied only 1 - 1,5 % of the wildebeest's time, while

drinking of water and suckling took up less than 0,5 % of total time.

4.4.1.3

Models of the activity of all major age-sex classes of wildebeest were constructed on a yearly and seasonal basis to illustrate the patterns followed from sunrise to sunset. A linear relationship between mean ambient temperature and the rate of inactivity (resting) was demonstrated statistically. The activity of a bull wildebeest in a mixed herd was recorded for 24 hours and showed distinct peaks and troughs in the major activity categories of resting, grazing and movement.

4.4.1.4

Statistical tests showed that significantly different amounts of time were spent by the various age-sex classes of wildebeest in resting, grazing, movement and social behaviour. The eight major age-sex and social classes measured in this way reflected considerable variation in especially the grazing component of activity. This was probably due to the nutritional demands made by growth, rutting, pregnancy and lactation, as well as the different grazing areas occupied by mixed herds and bull herds. Sub-

adult bulls spent 48 % of their time foraging and sub-adult cows 41 %. The remaining order of sequence was bachelor bulls (40 %), adult cows (36 %), bull calves (35 %), mixed herd bulls (32 %), lone, territorial bulls (29 %) and cow calves (19 %).

4.4.1.5

Strategies of mixed herds and bull herds in relation to obtaining food and water were compared on a seasonal basis. The most important findings were that mixed herds grazed less and moved more than bull herds. Mixed herds were also able to rest more. These temporal differences in activity may have been a result of mixed herds occupying better grazing areas, thereby lessening their foraging time and allowing them greater time for rest. However, because the areas of better grazing were situated farther from permanent water, the mixed herds were obliged to move greater distances to drink.

4.4.1.6

Diurnal and nocturnal scans of mixed herds and bull herds made it possible to model the 24-hour cycle of activity on a seasonal basis. Differences in diurnal and nocturnal activity were readily apparent and definite peaks and

troughs of activity were found in relation to season. Several environmental cues were probably responsible for the intrinsic activity patterns in wildebeest. Photoperiod appeared to be a crucial factor which determined the peaks of activity at dawn and dusk. Temperature, on the other hand, largely determined the diurnal period of inactivity. Thus photoperiod and temperature may have acted in combination as proximate factors in the determination of activity regimes, while other extrinsic factors, such as predators, may have impinged on the basic pattern, modifying it. Predator evasion at waterholes during the dry season appeared to be a factor affecting the activity of wildebeest at Etosha. Moreover, other intrinsic and extrinsic factors, not evaluated here, may have masked the original activity pattern and created variables in it which make interpretation difficult. Nevertheless, the synchrony within wildebeest herds was always apparent and could be quantitatively demonstrated during a study of the 24-hour cycle of activity.

4.4.1.7

Studies on the activity of wildebeest were found to be relevant to their management by helping to identify factors which may have limited the population. Furthermore, the particular requirements of the various age-sex

and social classes could be analysed to provide baseline data for calculating their respective energy budgets.

4.4.2 Hypothesis

Wildebeest at Etosha exhibit a fairly well-defined activity pattern which fluctuates predictably in relation to day and night and the seasons. Like most of the large ungulates, wildebeest are diurnally most active. Two of the more obvious extrinsic factors which act as proximate determinants of the basic pattern of activity are photoperiod and temperature. A third factor, namely predator evasion, acts as a modifying agent of this basic pattern. Intrinsic factors influencing the activity of wildebeest are age-sex class, reproductive condition and social status. The activity patterns in wildebeest indicate that nutrition was not a limiting factor for the population because, on average, grazing occupied one-third of the total time, while more than half of the total time was spent resting, including rumination. Being a ruminant, the frequent intake of food, followed by a period of rest and rumination, is a characteristic common to all phases of wildebeest activity.

Section 5

ENERGY BUDGET

5.1 INTRODUCTION AND TERMINOLOGY

Quantitative determination of carrying capacity in a conservation area for wild animals is very complex, since any system involving plants and animals is dynamic (Moen, 1973). To arrive at any meaningful conclusions about the number of animals which can be supported by a finite area, the energy requirements of that animal species for maintenance and reproduction must be known. In order to test whether sufficient energy is available to a population, the biomass of that population must be available (Petrusewicz and Macfayden, 1970). Consequently the ratios of age-sex classes and even social status of the species will affect the final estimate of biomass (Duncan and Klekowski, 1975).

In the present study, my main interest centred on an analysis of how much energy the wildebeest population at Etosha used on a seasonal and yearly basis, and whether there was sufficient production of energy by the grasslands to support this population. Obviously, provision must also be made

for the energy take-off by food competitors of wildebeest. This partitioning of resources between the major grass-eating herbivores will be discussed separately (Section 8). I propose to construct an energy budget for wildebeest by referring to their activity patterns (Section 4) and allocating theoretical values to the various activities. In addition to calculating the energy required for maintenance and activity, allowance was made for the phenomena of growth, gestation, lactation and homeothermy, all of which use energy.

Literature on energy use by free-ranging wildebeest is scant. Watson (1967) discussed an energy flow model in the Serengeti ecosystem, which included wildebeest. However, since little quantitative data were available, he limited this to a theoretical discussion. He states for instance that his figure for plant biomass "has been computed making the very considerable assumption . . .", and later that "although involving a good deal of speculation . . ." the wildebeest occupies an important position in the ecosystem. In a subsequent study of large ungulates in the Serengeti, wildebeest were found to have a relative maintenance requirement 5,22 times that of the standard unit (1,0) set for Thompson's gazelle (Bell, 1969). A tame wildebeest which was fed hay at different levels of nutrition, showed a resting metabolic

rate of 104,3 kcal/kg body mass ^{0,73}, which was 23 % more than the standard interspecific mean of 70 kcal/kg ^{0,75} (Rogerson, 1966, 1968). He also demonstrated that a tame wildebeest utilised corrected, metabolisable energy for maintenance with an efficiency of over 80 %, which is comparable to domestic cattle (Rogerson, 1968). Wildebeest also formed part of a community study of free-ranging large ungulates in which energetics were studied (Hirst, 1975). He found that the overall energy required by the grazing component was 223,5 kcal/m^2/year.

For the sake of clarity and precision, terminology must first be clearly defined. The terms used in this discussion are based on Standard International units (S.A. Bureau of Standards, 1973, 1976) and are also taken from Flatt (1970) and Moen (1973).

They are :

(a) Mass

The quantity of matter contained by a body, expressed in grams (g) or multiples thereof.

(b) Prefixes

When working with large amounts, the multiples

used are :

tera - (T) = 10^{12}
giga - (G) = 10^{9}
mega - (M) = 10^{6}
kilo - (k) = 10^{3} (viz. kilojoules or kJ).

(c) Gross Energy (GE)

The amount of heat released by complete oxidation of a substance.

(d) Digestible Energy (DE)

The total feed energy intake (GEi) minus faecal energy lost (FE).

(e) Total Digestible Nutrients (TDN)

The digestible protein plus digestible carbohydrates plus 2,25 times the digestible fat.

(f) Metabolisable Energy (ME)

The DE minus the urine energy (UE) minus the energy in the gaseous products of digestion (GPD).

(g) Net Energy (NE)

The difference between metabolisable energy and

heat increment (HI) following consumption of food in a thermoneutral environment. It includes the heat of fermentation (HF) and the heat of nutrient metabolism (HNM). Net energy is therefore the most refined measurement of how adequately the absorbed nutrients meet the metabolic needs of the animal.

(h) Thermal Neutral Zone (TNZ)

The air temperature range within which an endothermic animal is not required to thermoregulate physiologically.

(i) Resting Metabolic Rate (RMR)

The minimal energy cost when an animal is at rest within the TNZ and in a post-absorptive condition. It is a baseline of energy expenditure against which the increased energy requirements of activity, growth, gestation, lactation and homeothermy can be measured. The term RMR has been chosen in preference to BMR (basal metabolic rate) because the latter implies a condition of complete rest, seldom achieved in animal calorimetry.

5.2 METHODS

5.2.1 Calculation of Biomass

Estimation of the total wildebeest population at Etosha during 1977/78 was based on an aerial census done by helicopter in March 1978 (Section 12). Since wildebeest are usually undercounted by this method (Melton, 1978a), the estimate may be regarded as a minimum figure. It was not possible to accurately distinguish between the major age-sex classes of wildebeest during an aerial census and I therefore carried out ground counts at waterholes where a representative sample of the total population (31 %) drank. The ground counts were done in May, when limited availability of drinking water confined wildebeest to the proximity of perennial fountains. Although the aerial census was probably an underestimate, it was carried out when the population was at its annual peak, namely at the end of the calving period. These two errors are therefore compensatory and the final estimate of population size can be considered a realistic compromise and within the boundaries of the annual fluctuation in numbers.

Having satisfied requirements for total population size and its composition, I applied the mean body mass for each of the major age-sex and social classes of wildebeest,

using data obtained from 60 immobilised animals. This combination gave the estimated live mass of Etosha's wildebeest population during the 1977/78 season.

5.2.2 Allocation of Energetic Costs

The activity patterns of wildebeest at Etosha during 1977/78 have been discussed in detail in Section 4. In the case of marked wildebeest, I was able to distinguish between 13 specific categories of activity. Assuming an RMR as $70W_{kg}^{0,75}$ kcal.day^{-1} (National Research Council, 1966), I allocated the increased metabolic cost to each activity which required additional energy expenditure. It was thereby possible to eventually calculate the energetic cost of free existence to a wildebeest, on a daily basis.

5.2.2.1 Energy Requirements for Resting, Lying

Sternal recumbency is a standard requirement during a measurement of RMR and its energy requirement will therefore be 1,0 times $70W_{kg}^{0,75}$ kcal.day^{-1} (Moen, 1973). In wildebeest, the activity category of "resting, lying" met the major requirements of RMR except that field conditions did not always include the TNZ. Additional requirements for an ideal RMR include a post-absorptive digestive condition and "a calm psychological state"

(Moen, 1973). These obviously cannot yet be measured in free-ranging wildebeest. Rumination also occupies a definite role in the "resting, lying" category (Section 4.3.5.1) and an ever-present alertness for predators may preclude complete calm in a wild animal. Nevertheless for the purposes of this study, the activity category "resting, lying" was considered equal to RMR.

5.2.2.2 Energy Requirements for Resting, Standing

According to Crampton and Harris (1969) the increased energy expenditure of "resting, standing" is 9 % higher than RMR. Thus the increased energy requirement allocated in the present study was 1,1. Similar to the limitation imposed by field conditions on RMR, the actual cost of "resting, standing" in free-ranging wildebeest can only approximate the laboratory-based equation I applied.

5.2.2.3 Energy Requirements for Grazing

Although I distinguished between "grazing, stationary" and "grazing, moving" in the field, the two can be regarded as equal in terms of energy requirement (Graham, 1964). However, because the present study also recorded "walking" as a distinct activity, I decided to combine "grazing,

moving" with "walking". Only stationary grazing will be considered here. Using Graham's (1964) experiments on sheep as a basis, an increment of 1,59 on RMR was applied for time spent grazing.

5.2.2.4 Energy Requirements for Grazing, Moving and Walking

The flat terrain which wildebeest inhabit at Etosha requires that only energy expenditure for level movement need be considered. Using the findings of Clapperton (1961) for sheep as a reference, a value of 1,64 x RMR was assigned to grazing with purposeful movement and walking in wildebeest.

5.2.2.5 Energy Requirements for Trotting and Galloping

Wildebeest spent only 0,1 % of their time trotting and 0,6 % galloping (Section 4.3.5.1). This compares very favourably with the findings of Struhsaker (1967) who reported that the amount of time that elk spend running is less than 1 %. Hammel (1962) measured the energy cost of running in reindeer and found that the increment in energy requirement was 8,0 x RMR. This value was applied to the energy budget of wildebeest but contributes a relatively insignificant amount to the total.

5.2.2.6 Energy Requirements for Shading, Lying

The fact that wildebeest sought shade, indicated that they were encountering air temperatures in excess of the TNZ. I have assumed that "shading, lying" is the equivalent of "resting, lying" and thus equals RMR for the purpose of calculating energy requirements.

5.2.2.7 Energy Requirements for Shading, Standing

Similarly, a value of 1,1 x RMR was allocated to the energy cost of "shading, standing".

5.2.2.8 Energy Requirements for Drinking Water

The body posture of wildebeest when drinking water was very much the same as when they grazed in a stationary position. It was considered reasonable to assign the energy cost of grazing, namely 1,59 x RMR, to the drinking of both seasonal and perennial water. The actual time spent in drinking was only 0,3 % of the wildebeest's diurnal activity (Section 4.3.5.1) and the impact this had on total energy requirements was very small.

5.2.2.9 Energy Requirements for Suckling and Social Encounters

Again, total time spent in suckling (0,1 %) and overt social encounters (0,9 %) was low (Section 4.3.5.1). The method of collecting activity data in the focal-animal study (Section 4.3.1.3) excluded the running component of "social encounters". Therefore I applied a factor of 2,0 x RMR for both "suckling" and "social encounters". This is not nearly as high as "running" (8,0) but considerably higher than "walking" (1,64). Nevertheless the running component in social encounters was sufficiently small to be excluded. My criteria for social encounters also included all forms of territorial, fighting, threat, dominance, submissive, displacement and excitement displays (Section 4.2.1; Table 4.2). I was, however, unable to trace a collective energy cost allocation to these displays in the literature. The factor of 2,0 x RMR is thus the most arbitrary of the allocations made, but it was selected on the basis of field observation and experience. In any event, only 1 % of total time was spent in this category.

5.2.2.10 Energy Requirements for Growth, Pregnancy, Lactation and Homeothermy

In addition to maintenance and activity, homeotherms

require energy for growth, reproduction and thermoregulation.

(a) Growth

To estimate the energy required for growth from birth to adulthood, I used the formula $ME = 62W^{0,75}\ (1 + 0,60\ dg)$ given by Maynard and Loosli (1962), where :

ME = metabolisable energy in kcal
W = mass in lbs
dg = daily gain in mass (lbs)

The expression $62W^{0,75}$ represents the energy required for maintenance and activity and the expression in parentheses gives the growth requirement.

(b) Gestation

To calculate the energy requirements for gestation, the following equation (Moen, 1973) was used as a basis :

$$Q_{ep} = \left[e^{(2,8935 + 0,0174t_d)}\right]/_{bm}$$

where Q_{ep} = energy requirements on the particular, single day selected within the gestation period per kg foetus mass at term

e = natural logarithm

t_d = number of days pregnant, namely any single day selected within the gestation period

bm = birth mass of standard (domestic calf) in kg = 45

If the above equation is integrated to give the total area under the curve of the exponential increase in energy required for gestation by wild ruminants, then :

$$\int_0^t Q.t_d = \int_0^t e^{2,8935 + 0,0174t_d/bm.\ t_d}$$

$$= \frac{c.e^{2,8935}}{bm.\ 0,0174}\left[e^{0,0174t/c} - 1\right]$$

where $c = \frac{\text{gestation period in wildebeest}}{\text{gestation period in standard (domestic cattle)}}$

$= \frac{260}{280}$ days

$= 0,92857$

and t = total gestation period of wildebeest

= 260 days

(c) Lactation

The energy required for milk production was calculated by employing the formula provided in Moen (1973) :

$$Qel = \frac{\left[(RE_{ma})\,(RE_g)\,(70)\,(W_{kg}^{0,75})\right]\left[(RD)\,(1/E_{net})\right]}{GE_m}$$

where Qel = lactation based on energy requirements

RE_{ma} = energy increment for maintenance and activity of the calf

RE_g = energy increment for growth by the calf

RD = rumen development

E_{net} = net energy coefficient for milk

GE_m = energy in milk = no. $kcal.g^{-1}$

(d) Homeothermy

Unless wildebeest occupy the TNZ, they are in a critical thermal environment and will respond to maintain homeothermy (Moen, 1968). For a practical assessment of the energy required for homeothermy, I used the postulated linear relationship between air temperature and increment in RMR (Bartholomew, 1968). He states that

> "the slope of the curve relating heat production to ambient temperatures below the TNZ often extrapolates to a temperature equal to the core body temperature".

(e) Parasites

No quantitative data exist on the energy cost of a parasite or pathogen load to an animal (Moen, 1973) and I have not been able to trace published data on this parameter since then. In the case of Etosha's wildebeest the energy lost

to parasites or pathogens is probably small (Section 10) and for the purpose of this study it was ignored.

5.2.3 Calculation of Population Energy Budget

Energy requirements of a herd or population of animals is defined as the sum of the energy requirements of its individual members (Moen, 1973). He also specifies that since each individual's mean energy requirement is non-linear with respect to its body mass, the sum of the total energy cost to an individual must be determined. I have therefore taken cognizance of the energy requirements for the various age-sex and social classes in which wildebeest occur in the free-living state. Based on this premise, the population energy budget is :

$$TE_{wp} = \sum_{i=1}^{N} \left[E(m+a+g+r+h_1)(n_1) + E(m+a+g+r+h_n)(n_n) \right]$$

where TE_{wp} = total energy budget of the wildebeest population

$E(m+a+g+r+h)$ = sum of the energy requirements for maintenance, activity, growth, reproduction, homeothermy in a particular age-sex and social class (i=1 to N)

n = number of wildebeest in a particular age-sex and social class (i=1 to n).

5.2.4 Corrected Energy Requirements for a 24-Hour Cycle of Activity

The diurnal and nocturnal activity patterns in wildebeest differed (Section 4.3.6.4; Fig. 4.16). However, the allocation of energetic costs has been based on diurnal activity only (Section 4.2.3). To allow for the dissimilar diurnal and nocturnal activities of wildebeest, I applied a simple correction factor. Since the activity studies, on average, divided the day and night equally (Section 4.3.6.4; Figs 4.11 to 4.14), I calculated a correction factor for each activity category based on the difference between the 12 hours of diurnal activity and 12 hours of nocturnal activity. The relative energy cost for each activity (Section 5.2.2) was then adjusted for the nocturnal period using this correction factor. The corrected 24-hour energy budget must be regarded as an initial approximation for two reasons. Firstly, all nocturnal activity data were collected during full moon periods and so the calculated activity of wildebeest may not be representative of dark nights (Section 4.3.6.4). Secondly, the diurnal focal-animal studies distinguished 13 activity categories (Section 4.2.1), while the nocturnal scans of herds only made allowance for seven activity categories (Section 4.2.2). These seven categories combined the more detailed diurnal categories.

For example, in the daytime focal studies I distinguished between "resting, lying" and "resting, standing", but during nighttime scans these two categories were combined and I recorded only "resting". In addition, because of the limitations imposed by nocturnal activity studies, it was also decided to construct two separate energy budgets for the population, namely, a diurnal energy budget and a corrected energy budget for a 24-hour cycle of activity.

5.3 RESULTS AND DISCUSSION

5.3.1 Live Mass of Wildebeest Population

The live mass of Etosha's wildebeest population during 1977/78 has been estimated from data given in Table 5.1. During ground counts at waterholes I was able to distinguish nine different age-sex and social classes of wildebeest. A tenth class, namely lone, territorial bulls could be identified during aerial census. In the calculation of live mass, these 10 classes, together with the percentage of total population they represent have been listed. The mean mass of each class, with the exception of calves, was calculated from immobilised animals whose sex and social status were known. Age was estimated from tooth impressions taken during immobilisation.

Table 5.1 : Calculation of biomass for 10 age-sex and social classes of wildebeest at Etosha during 1977/78

Sex-Age and Social Class	% of Total Population	Number in Population	Mean Body Mass (kg)	Live Mass (Body Mass x Number)	% of Population Biomass
Calves (0-1 year)	20	498	65	32 370	7,2
Immature cows (1-2 years)	7	175	136	23 800	5,3
Immature bulls (1-2 years)	6	150	144	21 600	4,8
Sub-adult cows (2-3 years)	6	150	174	26 100	5,8
Sub-adult bulls (2-3 years)	4	98	207	20 286	4,5
Adult, lone territorial bulls	5	125	232	29 000	6,4
Adult, mixed herd bulls	3	75	241	18 075	4,0
Adult, bachelor bulls	16	399	250	99 750	22,1
Adult, non-pregnant cows	3	75	183	13 725	3,0
Adult, pregnant cows	30	748	223	166 804	36,9
		Σ_1 = 2 493		Σ_2 = 451 510	

Mean wildebeest body mass = Σ_2/Σ_1 = 181,11 kg

This method was sufficiently accurate to differentiate between calves, immatures, sub-adults and adults on the basis of tooth eruption and early wear.

Body mass of newborn calves could not be obtained and so I have relied on data from other areas. White-bearded wildebeest in East Africa have a lower birth mass than blue wildebeest in South Africa. Talbot and Talbot (1963) give a birth mass of 18,6 kg for bulls and 14,5 kg for cows while Watson (1967) mentions 16 kg in the case of white-bearded wildebeest. In South Africa, Kruger Park wildebeest were born at 21,74 kg (Braack, 1973) and in Zululand their birth mass approximated 24 - 25 kg (Attwell, 1977). I have accordingly taken an average from the latter two areas, namely 23 kg, and this may be a minor source of error in my estimation of mean mass for calves. Furthermore, I did not attempt to sex calves for the calculation of live mass because the body mass of immobilized yearlings was the same for both sexes (107 kg).

In Table 5.1 the body mass of each class has also been expressed as a percentage of the population live mass. From this it can be seen that pregnant, adult cows contributed the greatest live mass to the population. They also comprised the greatest percentage in terms of numbers. Second to them were the bachelor bulls. Calves

contributed the third highest live mass to the population, although their numbers predictably exceeded those of the bachelor bulls. The remaining sequence of live mass contribution was lone, territorial bulls, sub-adult cows, immature cows, immature bulls, sub-adult bulls, mixed herd bulls and lastly non-pregnant, adult cows.

The mean live mass of wildebeest at Etosha in 1977/78 was 181,11 kg. It compares favourably with a similar calculation for the wildebeest in Zululand of 174,05 kg (Attwell, 1977). In Kruger Park, the mean body mass of wildebeest is given as 181,4 kg (Pienaar *et al.*, 1966), 189,4 kg (Young *et al.*, 1969), 200,4 kg (Braack, 1973). However, the mean live mass of the white-bearded wildebeest in East Africa as computed from data of Talbot and Talbot (1963) is lower (168,4 kg). Employing Watson's (1967) figures, I obtained an even lower value of 150 kg for the Serengeti wildebeest. Thus my estimate for Etosha's wildebeest lies within the findings for South African populations, but is well above those of the East African populations, which are a separate subspecies (Section 1).

Previous workers have applied the "average" live mass value when evaluating "carrying capacity" or "stocking rate" (i.e. Braack, 1973; Attwell, 1977). I have approached this problem by calculating the energy requirement

separately for each of five major classes of wildebeest which I distinguished during the study of activity patterns (Section 4). These five classes were determined by practical considerations in the field and represent a combination of the more detailed classes listed in Table 5.1. They are : calves, immature and sub-adult bulls (1 - 3 years), immature and sub-adult cows (1 - 3 years), adult bulls and adult cows. I allocated the energy cost for the particular activities recorded in each class and then multiplied the results by the number of animals occupying each class. Finally, the energy requirements for the five classes were summed to give the energy budget of the population. I consider this method to be justified in view of the increased accuracy it provides when compared against "average" live mass values. This is made especially apparent when it is considered that the relationship of energy requirements is not linear to body mass of an animal (Moen, 1973).

5.3.2 Yearly Energetic Cost of Maintenance and Activity to Five Major Age-Sex and Social Classes

5.3.2.1 Calves

To simplify discussion, the steps required to calculate energetic costs have been set out in sequence in Table

5.2. I propose to justify each sequence of the calculations.

(a) Activity Categories

A total of 13 specific activity categories were used (Section 4.2.1; Table 5.2). These categories were chosen to include all overt social and non-social behaviour of wildebeest.

(b) Energy Cost Factor for Activity

The unit of energy cost was based on a standard RMR equation of $70W_{kg}^{0,75}$ (Section 5.2.2). In the case of calves, it was $70 \times 65^{0,75}$ kcal.day^{-1} = 1 602,44 kcal.day^{-1}. The energy cost factor for each activity was discussed in Sections 5.2.2.1 to 5.2.2.9.

(c) Metabolic Cost per Hour

This was calculated in kcal on an hourly basis by dividing the energy cost factor of RMR by 24 hours.

(d) Percentage of Day Spent on Activity

I obtained this information from the detailed activity data which were computed as indicated in Section 4.2.1 : Appendices 4 and 5.

able 5.2 : Diurnal energy budget for maintenance and activity in wildebeest calves at Etosha during 1977/78, corrected for a 24-hour cycle of activity

Activity	Energy Cost Factor for Activity (1,0 Unit = RMR)	Metabolic Cost (kcal/h)	% of Day Spent on Activity	Activity in Hours per 12 Hour Day	Diurnal Cost (kcal/12h)	Gross 24 h Cost (kcal)	Correction Factor for Nocturnal Activity	Nocturnal Cost (kcal/12h)	Corrected Energy Budget for a 24 h Cycle of Activity
sting, ying	1,00	66,77	46,15	5,54	369,91	739,82	1,13	418,00	787,91
sting, tanding	1,10	73,45	16,42	1,97	144,70	289,40	1,13	159,17	303,87
azing, tationary	1,59	106,16	18,03	2,16	229,31	458,62	1,05	240,78	470,09
azing, oving	1,64	109,50	1,51	0,18	19,71	39,42	1,05	20,70	40,41
lking	1,64	109,50	10,95	1,31	143,45	286,90	0,39	55,95	199,40
otting	8,00	534,15	0,06	0,01	5,34	10,68	0,39	2,08	7,42
lloping	8,00	534,15	0,63	0,07	37,39	74,78	0,39	14,58	51,97
ading, ying	1,00	66,77	3,56	0,43	28,71	57,42	None	0,00	28,71
ading, tanding	1,10	73,45	1,75	0,21	15,42	30,84	None	0,00	15,42
inking easonal ater	1,59	106,16	0,05	0,01	1,06	2,12	1,00	1,06	2,12
inking erennial ater	1,59	106,16	0,11	0,02	2,12	4,24	None	0,00	2,12
ckling	2,00	133,54	0,31	0,03	4,01	8,02	1,00	4,01	8,02
cial ncounters	2,00	133,54	0,56	0,06	8,01	16,02	0,57	4,57	12,58
			Σ_1=100	Σ_2=12,00	Σ_3=1 009,14	Σ_4=2 018,28		Σ_5 = 920,90	$\Sigma_3+\Sigma_5$=1 930,04
					4 222,24J	8 444,48J		3 853,05J	8 075,29J
				J.year^{-1}	1 541 118J	3 082 235J	J.year^{-1}	1 406 363J	2 947 480J

(e) Activity in Hours per 12-Hour Day

The percentage of day spent on a particular activity was multiplied by a factor of 12.

(f) Diurnal Cost

This was calculated in kcal for an average diurnal period of 12 hours by multiplying the metabolic cost per hour by the number of hours spent in a particular activity.

(g) Gross 24-Hour Cost

Calculated in kcal, it represented double the diurnal cost, assuming that diurnal and nocturnal activities were equal. However, because they were unequal, the result was only given for purposes of comparison with the corrected energy budget for a 24-hour cycle of activity.

(h) Correction Factor for Nocturnal Activity

This was an approximation and must remain arbitrary until techniques are developed for recording all nocturnal activity in wildebeest. I obtained the correction factor from diurnal and nocturnal scans (Section 4.3.6.4), the limitations of which have been discussed (Section 5.2.4).

(i) Nocturnal Cost

This was calculated in kcal for an average nocturnal period of 12 hours by multiplying the diurnal cost by the correction factor for a particular activity. In the case of certain activities, notably shading, a nocturnal cost cannot exist. However, in the case of drinking seasonal water, it does, although I did not record it (Section 4.3.6.4). I have therefore applied the diurnal value to the nocturnal drinking of seasonal water. In my experience, wildebeest never or very rarely drank from perennial fountains in Etosha at night because of predators. Consequently no nocturnal cost was allocated to this activity.

(j) Corrected Energy Budget for a 24-Hour Cycle of Activity

The total diurnal costs (Σ_3) and the total nocturnal costs (Σ_5) have been summed to give a 24-hour estimate of energy requirement.

(k) Comparison of the Diurnal, Nocturnal and Corrected Energy Budgets in Calves

When the 24-hour energy budget is related to the RMR for the same period, an expression of the relative energy cost of maintenance and activity in wildebeest calves is obtained.

Thus $RE_{ma} = \frac{Ema}{RMR}$

Where RE_{ma} = increment for maintenance and activity against RMR

Ema = total energy required during a 24-hour cycle of activity (kcal)

RMR = resting metabolic rate per 24-hour cycle of activity (kcal)

Therefore :

$$RE_{ma} = \frac{1\ 930,04}{1\ 602,44} = 1,20$$

Similarly, the diurnal RE_{ma} is 1,26 and the nocturnal RE_{ma} is 1,15. No estimates of this parameter in regard to free-ranging calves of African ungulates were found in the literature. However, several first approximations exist for North American ungulates (Moen, 1973) and have been calculated for sub-adult and adult animals. These will be referred to when I discuss the appropriate classes in wildebeest (Sections 5.3.2.3 to 5.3.2.5).

Although the corrected 24-hour energy budget for maintenance and activity presented here must be regarded as a first approximation, it will probably be found to lie between the values of the diurnal and nocturnal energy

budgets when improved techniques are available. This prediction is supported by the fact that there was less nocturnal activity in wildebeest during full moon periods than in the diurnal period. Consequently the nocturnal energy budget is closer to RMR. Studies on Thompson's gazelle indicate that activity on moonless nights declines further (Walther, 1973) and so it may well be that the mean nocturnal energy budget in wildebeest will be lower than presented here.

(1) Conversion of Energy Budget for Maintenance and Activity to Joules per Annum

Since the existing formula for calculating RMR is expressed in kcal and the majority of literature used "calorie" as a unit of energy, I have retained it in my construction of an annual energy budget for maintenance and activity. The joule conversion factor of 4,184 has been applied to the total energy budget and the resultant figures are given as joules per annum ($J.yr^{-1}$), in order to comply with SI standards.

5.3.2.2 Immature and Sub-Adult Cows

Similar calculations were made to express the yearly energy budget for maintenance and activity in wildebeest cows aged one to three years. The results are shown in

Table 5.3. Based on an RMR of 70 x $155^{0,75}$ kcal.day^{-1} = 3 075,01 kcal.day^{-1}, the diurnal RE_{ma} is 1,33 and the nocturnal RE_{ma} is 1,28. For the corrected energy budget of 24 hours the RE_{ma} = 1,30. As in the case of calves, this appears to be the first analysis of energy budgets which have been undertaken on free-ranging African ungulates, using quantitative activity data as a baseline. Moen (1973) discusses similar first approximations, but the deer and elk he refers to do not include immature females.

5.3.2.3 Immature and Sub-Adult Bulls

The yearly energy budget for maintenance and activity in wildebeest bulls aged one to three years appears in Table 5.4. The RMR is 70 x $175,5^{0,75}$ kcal.day^{-1} = 3 375,25 kcal.day^{-1}. Diurnal RE_{ma} is 1,40 and nocturnal RE_{ma} is 1,32. For a corrected energy budget of 24 hours, the RE_{ma} is 1,36. Although no parameter of this nature exists for free-ranging African ungulates, a corresponding value of 1,44 was found in a 145 kg elk spike bull in velvet (Moen, 1973). This animal had a RMR of 2 925 kcal. day^{-1}, which is in proportion to my estimate for immature and sub-adult bull wildebeest. The data on immature elk referred to by Moen (1973) were collected diurnally. Thus, if the RE_{ma} of elk (1,44) is compared against the

Table 5.3 : Diurnal energy budget for maintenance and activity in immature and sub-adult wildebeest cows at Etosha during 1977/78, corrected for a 24 hour cycle of activity

Activity	Energy Cost Factor for Activity (1,0 Unit = RMR)	Metabolic Cost (kcal/h)	% of Day Spent on Activity	Activity in Hours per 12 Hour Day	Diurnal Cost (kcal/12h)	Gross 24 h Cost (kcal)	Correction Factor for Nocturnal Activity	Nocturnal Cost (kcal/12h)	Corrected Energy Budget for a 24 h Cycle of Activity
esting, lying	1,00	128,13	36,16	4,34	556,08	1 112,16	1,13	628,37	1 184,45
esting, standing	1,10	140,94	15,36	1,84	259,33	518,66	1,13	293,04	552,37
razing, stationary	1,59	203,72	28,88	3,46	704,87	1 409,74	1,05	740,11	1 444,98
razing, moving	1,64	210,13	5,48	0,66	138,69	277,38	1,05	145,62	284,31
alking	1,64	210,13	13,48	1,62	340,41	680,82	0,39	132,76	473,17
rotting	8,00	1 025,00	0,02	0,01	10,25	20,50	0,39	4,00	14,25
alloping	8,00	1 025,00	0,24	0,03	30,75	61,50	0,39	11,99	42,74
hading, lying	1,00	3 075,01	0,00	0,00	0,00	0,00	0,00	0,00	0,00
hading, standing	1,10	140,94	0,00	0,00	0,00	0,00	0,00	0,00	0,00
rinking seasonal water	1,59	203,72	0,08	0,01	2,04	4,08	1,00	2,04	4,08
rinking perennial water	1,59	203,72	0,00	0,00	0,00	0,00	0,00	0,00	0,00
uckling	2,00	256,25	0,00	0,00	0,00	0,00	1,00	0,00	0,00
ocial encounters	2,00	256,25	0,30	0,03	7,69	15,38	0,57	4,38	12,07
			Σ_1=100	Σ_2=12,00	Σ_3= 2 050,11	Σ_4=4 100,22		Σ_5=1 962,31	$\Sigma_3+\Sigma_5$=4 012,42
					8 577,66J	17 155,32J		8 210,31J	16 787,97J
				J.year^{-1}	3 130 846J	6 261 692J	J.year^{-1}	2 996 763J	6 127 607J

Table 5.4 : Diurnal energy budget for maintenance and activity in immature and sub-adult wildebeest bulls at Etosha during 1977/78, corrected for a 24 hour cycle of activity

Activity	Energy Cost Factor for Activity (1,0 Unit = RMR)	Metabolic Cost (kcal/h)	% of Day Spent on Activity	Activity in Hours per 12 Hour Day	Diurnal Cost (kcal/12h)	Gross 24 h Cost (kcal)	Correction Factor for Nocturnal Activity	Nocturnal Cost (kcal/12h)	Corrected Energy Budget for a 24 h Cycle of Activity
sting, ying	1,00	140,64	23,89	2,87	403,64	807,28	1,13	456,11	859,75
sting, tanding	1,10	154,70	16,17	1,94	300,12	600,24	1,13	339,14	639,26
azing, tationary	1,59	223,61	38,08	4,57	1 021,90	2 043,80	1,05	1 073,00	2 094,90
azing, oving	1,64	230,64	6,20	0,74	170,67	341,34	1,05	179,20	349,87
lking	1,64	230,64	14,01	1,68	387,48	774,96	0,39	151,12	538,60
otting	8,00	1 125,08	0,01	0,01	11,25	22,50	0,39	4,39	15,64
lloping	8,00	1 125,08	0,23	0,02	22,50	45,00	0,39	8,78	31,28
ading, ying	1,00	140,64	0,13	0,01	1,41	2,82	None	0,00	1,41
ading, tanding	1,10	154,70	0,00	0,00	0,00	0,00	None	0,00	0,00
inking easonal ater	1,59	223,61	0,04	0,01	2,24	4,48	1,00	2,24	4,48
inking erennial ater	1,59	223,61	0,17	0,02	4,47	8,94	None	0,00	4,47
ckling	2,00	281,27	0,00	0,00	0,00	0,00	1,00	0,00	0,00
cial ncounters	2,00	281,27	1,07	0,13	36,56	73,12	0,57	20,84	57,40
			Σ_1=100	Σ_2=12,00	Σ_3=2 362,24	Σ_4=4 724,48		Σ_5=2 234,82	$\Sigma_3+\Sigma_5$=4 597,06
					9 883,61J	19 767,22J		9 350,49J	19 234,10J
				J.year^{-1}	3 607 518J	7 215 035J	J.year^{-1}	3 412 929J	7 020 446J

diurnal value obtained for wildebeest (1,40), the two are in close agreement. It should, however, be remembered that the activity categories in these two studies differed to some extent.

5.3.2.4 Adult Cows

The yearly energy budget for maintenance and activity in adult cows of three years and older is shown in Table 5.5. RMR is 70 x $219,36^{0,75}$ kcal.day^{-1} = 3 989,94 kcal.day^{-1}. In calculating the body mass of adult cows, I made allowance for non-pregnant and pregnant members of the population (Table 5.1). Diurnal RE_{ma} is 1,37 and nocturnal RE_{ma} is 1,22. RE_{ma} for a corrected energy budget of 24 hours is 1,29.

Using 24-hour observations on maintenance and activity of a free-ranging, 39 kg female white-tailed deer, the RE_{ma} ranged from 1,24 to 1,45, including the extremes of activity (Moen, 1973). My first approximation of 1,29 for adult wildebeest cows is within this range, although the activity categories applied in the two studies differed. The categories applied to white-tailed deer favoured a higher RE_{ma}, since the category of rumination, with an increment of 1,26 over RMR (Moen, 1973), was included. The percentage of time spent ruminating could

able 5.5 : Diurnal energy budget for maintenance and activity in adult wildebeest cows at Etosha during 1977/78, corrected for a 24 hour cycle of activity

Activity	Energy Cost Factor for Activity (1,0 Unit = RMR)	Metabolic Cost (kcal/h)	% of Day Spent on Activity	Activity in Hours per 12 Hour Day	Diurnal Cost (kcal/12h)	Gross 24 h Cost (kcal)	Correction Factor for Nocturnal Activity	Nocturnal Cost (kcal/12h)	Corrected Energy Budget for a 24 h Cycle of Activity
esting, ying	1,00	166,25	22,63	2,71	450,54	901,08	1,13	509,11	959,65
esting, standing	1,10	182,87	20,24	2,43	444,37	888,74	1,13	502,14	946,51
razing, stationary	1,59	264,33	31,71	3,80	1 004,45	2 008,90	1,05	1 054,67	2 059,12
razing, roving	1,64	272,65	4,63	0,56	152,68	305,36	1,05	160,31	312,99
lking	1,64	272,65	10,85	1,30	354,45	708,90	0,39	138,24	492,69
rotting	8,00	1 329,98	0,05	0,01	13,30	26,60	0,39	5,19	18,49
lloping	8,00	1 329,98	0,68	0,08	106,40	212,80	0,39	41,50	147,90
ading, ying	1,00	166,25	2,23	0,27	44,89	89,78	None	0,00	44,89
ading, standing	1,10	182,87	6,19	0,74	135,32	270,64	None	0,00	135,32
rinking easonal ater	1,59	264,33	0,06	0,01	2,64	5,28	1,00	2,64	5,28
rinking erennial ater	1,59	264,33	0,30	0,04	10,57	21,14	None	0,00	10,57
ckling	2,00	332,50	0,15	0,02	6,65	13,30	1,00	6,65	13,30
cial ncounters	2,00	332,50	0,28	0,03	9,98	19,96	0,57	5,69	15,67
			Σ_1=100	Σ_2=12,00	Σ_3=2 736,24	Σ_4=5 472,48		Σ_5=2 426,14	$\Sigma_3+\Sigma_5$=5 162,38
					11 448,43J	22 896,86J		10 150,97J	21 599,40J
				J.year^{-1}	4 178 677J	8 357 354J	J.year^{-1}	3 705 104J	7 883 780J

not be determined in free-ranging wildebeest during the present study (Section 4.3.5.1), and the inclusion of this parameter will therefore raise the RE_{ma} in wildebeest.

5.3.2.5 Adult Bulls

The yearly energy budget for maintenance and activity in adult bulls of three years and older is shown in Table 5.6. RMR is $70 \times 245,13^{0,75}$ kcal.day^{-1} = 4 336,56 kcal.day^{-1}. To calculate a mean body mass for the three social classes of adult wildebeest bulls, the proportion in which they occurred at Etosha was taken into consideration (Table 5.1). Diurnal RE_{ma} is 1,42, the nocturnal value is 1,25, and the value for a corrected energy budget of 24 hours is 1,34.

In North American elk the adult bulls' RE_{ma} was 1,74 - 1,75 (Moen, 1973). This is higher than the values obtained in wildebeest, however the difference may be explained by the inclusion of bachelor bull wildebeest in my data. The values obtained for elk were from solitary and harem bulls (Moen, 1973), which probably have greater activity than bull herds.

5.3.3 Energy Required for Growth

Growth in wildebeest, like all ungulates, is most rapid

Table 5.6 : Diurnal energy budget for maintenance and activity in adult wildebeest bulls at Etosha during 1977/78, corrected for a 24 hour cycle of activity

Activity	Energy Cost Factor for Activity (1,0 Unit = RMR+)	Metabolic Cost (kcal/h)	% of Day Spent on Activity	Activity in Hours per 12 Hour Day	Diurnal Cost (kcal/12h)	Gross 24 h Cost (kcal)	Correction Factor for Nocturnal Activity	Nocturnal Cost (kcal/12h)	Corrected Energy Budget for a 24 h Cycle of Activity
sting, ying	1,00	180,69	24,92	2,99	540,26	1 080,52	1,13	610,49	1 150,75
sting, tanding	1,10	198,76	23,57	2,82	560,50	1 121,00	1,13	633,37	1 193,87
azing, tationary	1,59	287,30	26,73	3,20	919,36	1 838,72	1,05	965,33	1 884,69
azing, oving	1,64	296,33	3,77	0,45	133,35	266,70	1,05	140,02	273,37
lking	1,64	296,33	17,53	2,10	622,29	1 244,58	0,39	242,69	864,98
otting	8,00	1 445,52	0,04	0,01	14,46	28,92	0,39	5,64	20,10
lloping	8,00	1 445,52	0,97	0,12	173,46	346,92	0,39	67,65	241,11
ading, ying	1,00	180,69	0,00	0,00	0,00	0,00	None	0,00	0,00
ading, tanding	1,10	198,76	0,02	0,01	1,99	3,98	None	0,00	1,99
inking easonal ater	1,59	287,30	0,02	0,01	2,87	5,74	1,00	2,87	5,74
inking erennial ater	1,59	287,30	0,31	0,04	11,49	22,98	None	0,00	11,49
ckling	2,00	361,38	0,00	0,00	0,00	0,00	1,00	0,00	0,00
cial ncounters	2,00	361,38	2,12	0,25	90,35	180,70	0,57	51,50	141,85
			Σ_1=100	Σ_2=12,00	Σ_3=3 070,38	Σ_4=6 140,76		Σ_5=2 719,56	$\Sigma_3+\Sigma_5$=5 789,94
					12 846,47J	25 692,94J		11 378,64J	24 225,11J
				J.year^{-1}	4 688 962J	9 377 923J	J.year^{-1}	4 153 203J	8 842 165J

from birth to one year of age (Talbot and Talbot, 1963; Watson, 1967; Braack, 1973; Attwell, 1977). Because of apparent differences in body mass at birth which exist between white-bearded wildebeest and blue wildebeest (Section 5.3.1), I have limited my data base for the quantitative calculation of growth to findings in blue wildebeest.

Body mass at birth and average gain in mass per day were not directly determined during the present study. A body mass of 23 kg at birth has been assumed (Section 5.3.1). Daily gain in body mass from birth to one year was 0,247 kg (bulls) and 0,265 (cows) in Kruger Park wildebeest (Braack, 1973). In Zululand wildebeest it was 0,242 kg (bulls) and 0,248 kg (cows) (Attwell, 1977). Based on these figures and the body mass of yearlings at Etosha, I have applied a mean growth rate of 230 $g.day^{-1}$. At Etosha, yearling wildebeest had a body mass of 107 kg, which compared favourably with the mass of 115 kg in yearlings (Braack, 1973) and of 116 kg in yearlings (Attwell, 1977). Moreover, there appeared to be little difference in growth between sexes in calves (Talbot and Talbot, 1963; and this study), although females may be 6 kg heavier than males at the age of one year (Attwell, 1977; Braack, 1973). I assumed that the sexes grow at an equal rate from birth to one year of age.

From one to two years of age the rate of growth between the sexes differed. Cows gained 58 kg (107 - 165 kg) and bulls gained 74 kg (107 - 181 kg) as found during the measurement of 26 wildebeest. In Kruger Park the corresponding values were 57 kg and 55 kg respectively (Braack, 1973), while in Zululand values of 49 kg and 63 kg were obtained (Attwell, 1977). From two to three years of age this trend continued in the wildebeest at Etosha. Bulls in this age class gained 51 kg and cows gained 18 kg. Other workers were at variance in their findings on this increment. For instance, in Kruger Park, bulls gained 32 kg and cows gained 45 kg (Braack, 1973), while in Zululand bulls gained 40 kg and cows gained 18 kg (Attwell, 1977). My findings are consistent with those of Attwell (1977). In the present study I used mean values from Etosha for the combined age classes of immatures and sub-adults.

Applying the formula $ME = 62W^{0,75} (1 + 0,60\ dg)$ from Maynard and Loosli (1962) which was clarified in the method section (5.2.2.10), I obtained a first approximation of energy required for maintenance, activity and growth in Etosha's wildebeest population from birth to adulthood. The results are given in Table 5.7. Because these energy requirements still included the components of energy required for maintenance and activity, it was first

Table 5.7 : Energy required for growth, maintenance and activity in three major age-sex classes of wildebeest at Etosha (1977 - 78)

Age-sex class	Mean gain in body mass for 1 year (kg)	Mean daily gain in body mass (kg)	Energy required per wildebeest ($kcal.day^{-1}$)
Calves (0 - 1 year)	84	0,230	3 349,11
Immature & sub-adult cows (1 - 3 years)	38	0,104	5 605,51
Immature & sub-adult bulls (1 - 3 years)	63	0,172	6 649,92

necessary to subtract their energy cost.

In Table 5.8, the parameters Ema + Eg denote the energy requirements for maintenance and activity, plus growth as determined by the equation of Maynard and Loosli (1962). If the parameters Eg and RMR are expressed as a coefficient, then an estimate of the energy cost of growth in wildebeest can be obtained. A similar coefficient has been used to express the increment for maintenance and activity (RE_{ma} : Section 5.3.2.1).

Thus : $RE_g = \frac{Eg}{RMR}$

Where : RE_g = increment for growth

Eg = energy required for growth in a particular age-sex class (kcal)

RMR = energy required for maintenance (kcal)

Applying this formula to my estimates for growth cost in wildebeest (Table 5.8), the following predictions could be made. Calves required the greatest amount of energy in proportion to their body mass for growth, followed by immature and sub-adult bulls. Immature and sub-adult cows had the least energy requirement for growth. This sequence closely approximated the time spent in grazing by

Table 5.8 : Calculation of energy required for growth in three major age-sex classes of wildebeest at Etosha (1977 - 78)

Age-sex class	Parameters of energy *				
	Ema + Eg ($kcal.day^{-1}$)	Ema ($kcal.day^{-1}$)	Eg ($kcal.day^{-1}$)	RMR ($kcal.day^{-1}$)	Increment for growth (RE_g)
Calves (0-1 year)	3 349,11	1 930,04	1 419,07	1 602,44	0,89
Immature and sub-adult cows (1-3 years)	5 605,51	4 012,42	1 593,09	3 075,01	0,52
Immature and sub-adult bulls (1-3 years)	6 649,92	4 597,06	2 052,86	3 596,44	0,57

* Explanation in text

immatures and sub-adults of both sexes (Section 4.3.5.4). Calves, which had a relatively low level of grazing time, obviously obtain a considerable portion of their energy from milk.

5.3.4 Energy Required for Gestation

The energy cost of gestation had considerable influence on the population energy budget of wildebeest as the adult female component had a pregnancy rate of approximately 90 % (Section 12). In addition, increase in foetal mass in wildebeest in relation to gestation period is exponential (Braack, 1973; Attwell, 1977). By applying a modified equation which was based on that given by Moen (1973) (Section 5.2.2.10), I calculated the additional energy required by pregnant wildebeest cows at Etosha. To satisfy the equation, certain data are required. The gestation time in days of free-ranging wildebeest has been variously reported as 270 (Talbot and Talbot, 1963), 240 - 254 (Watson, 1967), *c.* 250 (Braack, 1973; Attwell, 1977). In the present study I was able to determine the gestation period in one adult, marked cow to be approximately 260 days. Furthermore, the body mass of a wildebeest calf at birth was assumed to be 23 kg (Section 5.3.1). The complete equation is :

$$Q_{ep} = \frac{0,92857 \times 2,718^{2,8935}}{45 \times 0,0174}\left[2,718^{0,0174 \times 260/0,92857} - 1\right]$$

$$= 2\ 772,56 \text{ kcal.day}^{-1}\text{.kg foetus mass at term}$$

$$= 2\ 772,56 \text{ kcal} \times 23 \text{ kg}$$

$$= 63\ 769 \text{ kcal.pregnancy}^{-1}$$

$$= 266\ 810 \text{ kJ.pregnancy}^{-1}$$

If the energy required for gestation is related to RMR, the coefficient is :

$$RE_p = \frac{Q_{ep}}{RMR}$$

where RE_p = increment for pregnancy

Q_{ep} = energy required for pregnancy (kcal)

RMR = energy required for maintenance (kcal)

Then $RE_p = \frac{63\ 769}{905\ 544}$

$= 0,07$

Note that this coefficient is derived by dividing the total energy cost of pregnancy by the total cost of RMR for the gestation period, namely $70.183^{0,75}$ x 260 days = 905 544 kcal. The relative cost of gestation in wildebeest (0,07) is lower, but similar to that calculated for white-tailed deer (0,11 : Moen, 1973). This may be due to the shorter gestation period of 200 days in deer.

5.3.5 Energy Required for Lactation

Two factors need to be considered when estimating the cost of lactation. Firstly, the energy contained in the milk must be determined and, secondly, the energy required by the lactating cow to produce the milk should be taken into account (Moen, 1973). To satisfy the equation described in Section 5.2.2.10, I applied the following data for wildebeest. Energy increment for activity of calves (RE_{ma}) was 1,20 (Section 5.3.2.1). Energy increment for production by calves (RE_g) was 0,89 (Section 5.3.3). The rumen development (RD) in free-ranging wildebeest calves has not been measured. However, in the case of white-tailed deer fawns, Moen (1973), calculated the following regression equation :

$$\% \text{ MD} = 113,6 - 4,5\ W_{kg}$$

where % MD = % of nutrients met by milk

W_{kg} = body mass of fawn

This equation is based on the premise that there is 100 % milk utilisation at birth and that it decreases to zero at weaning. Hence, the mean % MD was shown to approximate 50 % during the period from birth to weaning. The term RD expresses the regression equation in white-tailed

deer as a factor of % MD :

$$RD = \frac{113,6 - 4,5_{kg}}{100} \qquad \text{(Moen, 1973)}$$

For the purpose of this study I have assumed an RD factor of 0,5. This indicates that, on average, a calf will be 50 % dependent on milk from birth to weaning.

The net energy coefficient for wildebeest milk was set at 0,8 which is in keeping with other free-ranging ungulates (Moen, 1973). Finally, the energy contained by wildebeest milk, in $kcal.g^{-1}$, is used as the denominator in the equation. To determine this factor, eight milk samples were obtained from immobilised, lactating cows over a period of nine months. In addition, I took a milk sample from one cow, shot for veterinary investigation (Section 10). The composition of wildebeest milk is given in Section 7.3, Table 7.16. To calculate calorific values, I used 9,12 for fat; 5,4 for protein; 3,9 for carbohydrate (Durnin and Passmore, 1967). The sum of the calorific values is 146,64 kcal/100 g. Therefore, in the equation, I applied a value of 1,47 $kcal.g^{-1}$. This is more than double the energy found in milk of white-tailed deer, which was 0,7 $kcal.g^{-1}$ (Moen, 1973).

The final equation is :

$$Qel = \frac{(1,20 \times 0,89 \times 70 \times 65^{0,75})(0,5 \times \frac{1}{0,8})}{1,47}$$

$$= 727,64 \text{ kcal.day}^{-1}$$

$$= 3\ 044,45 \text{ kJ.day}^{-1}$$

Having made a first approximation of the amount of energy in wildebeest milk, I estimated the energy required by the lactating cow to produce this milk. Although a parameter of this nature has not been established for free-ranging ungulates (Moen, 1973), it has been determined for domestic stock. In dairy cattle the energy required for milk production is said to be more than 1,6 times the energy contained in the milk (Crampton and Harris, 1969). Applying this factor to wildebeest, the energy required to produce milk will be $1,6 \times 727,64 \text{ kcal.day}^{-1} = 1\ 164,22 \text{ kcal.day}^{-1}$, which represents the total energy involved in lactation.

If the cost of lactation is examined in relation to RMR, the coefficient is :

$$RE_1 = \frac{Qel}{RMR}$$

where RE_l = increment for lactation

Qel = total energy involved in lactation

RMR = energy required for maintenance

Then $RE_l = \frac{1\ 164,22}{3\ 482,86}$

$= 0,33$

The relative cost of lactation to wildebeest cows is therefore considerably higher than the relative cost of gestation (RE_g), which was estimated to be 0,07 (Section 5.3.4). However, when it is considered that gestation and lactation occur simultaneously for about 70 % of the year, the combined energy cost may be considerable. I will discuss this subsequently (Section 5.3.7).

Energy requirement for lactation in wildebeest is the same as for white-tailed deer with one fawn at peak lactation (RE_l = 0,33; Moen, 1973).

5.3.6 Energy Required for Homeothermy

An estimate of the energy needed to maintain homeothermy in wildebeest was made by relating air temperatures to increments of RMR, as outlined by Bartholomew (1968). However, because the TNZ in free-ranging wildebeest is

unknown, I chose an arbitrary range of 15 - 25 ^{o}C as representative of TNZ in wildebeest at Etosha. My criteria for this choice were based on observed behavioural responses to ambient temperatures above 25 ^{o}C and below 15 ^{o}C, which indicated that the animals were either off-loading or taking up heat outside this range. The effect of high incoming solar radiation on the dark pelage of wildebeest must be considerable because colour of the pelage is an important factor in absorption of radiant energy (Moen, 1973). Nevertheless, I have assumed that 15 ^{o}C is the lower range of the TNZ in wildebeest, considering that eland, a similar ungulate, but with a shorter, lighter coloured pelage, begin to thermoregulate below 20 ^{o}C (Taylor and Lyman, 1967).

I have only considered the energy required for maintenance of homeothermy when air temperatures declined below the TNZ, because the energy required for off-loading heat is minimal as a result of the well-developed behavioural responses of shading and orientation I observed in wildebeest.

I measured a core body temperature of 39 ^{o}C in immobilised and shot wildebeest. This temperature was then used to extrapolate the estimated increase in RMR through the selected lower critical temperature of 15 ^{o}C. In addition,

I extrapolated a hypothetical lower critical temperature (LCT) of 10 °C from the core body temperature to RMR (Fig. 5.1). I have taken 10 °C to represent the lowest parameter of LCT for comparative purposes because the minimum temperature at Etosha decreased below 10 °C for only 3,53 % of the year, as shown in Table 5.9. My intention was to compare the energetic cost of thermoregulation to wildebeest, using the mean minimum temperatures which occur below these two critical thermal parameters at Etosha. Moreover, I have used screen temperatures which were recorded during the study of activity patterns in wildebeest (Section 4), for these determinations.

Table 5.9 shows the calculation of the amount of time, over a period of one year, when temperatures at Etosha decreased to below 10 °C and 15 °C respectively. Daily readings were taken to the nearest hour for this purpose, using a recording thermograph. The mean minimum temperatures below the 10 °C and 15 °C levels were 8,3 °C and 9,8 °C and occurred for 3,53 % and 15,47 % of the year, respectively.

Applying these results to Fig. 5.1, I found that a mean minimum temperature of 8,3 °C using an LCT of 10 °C would result in a 3 % increment over RMR. Likewise, a

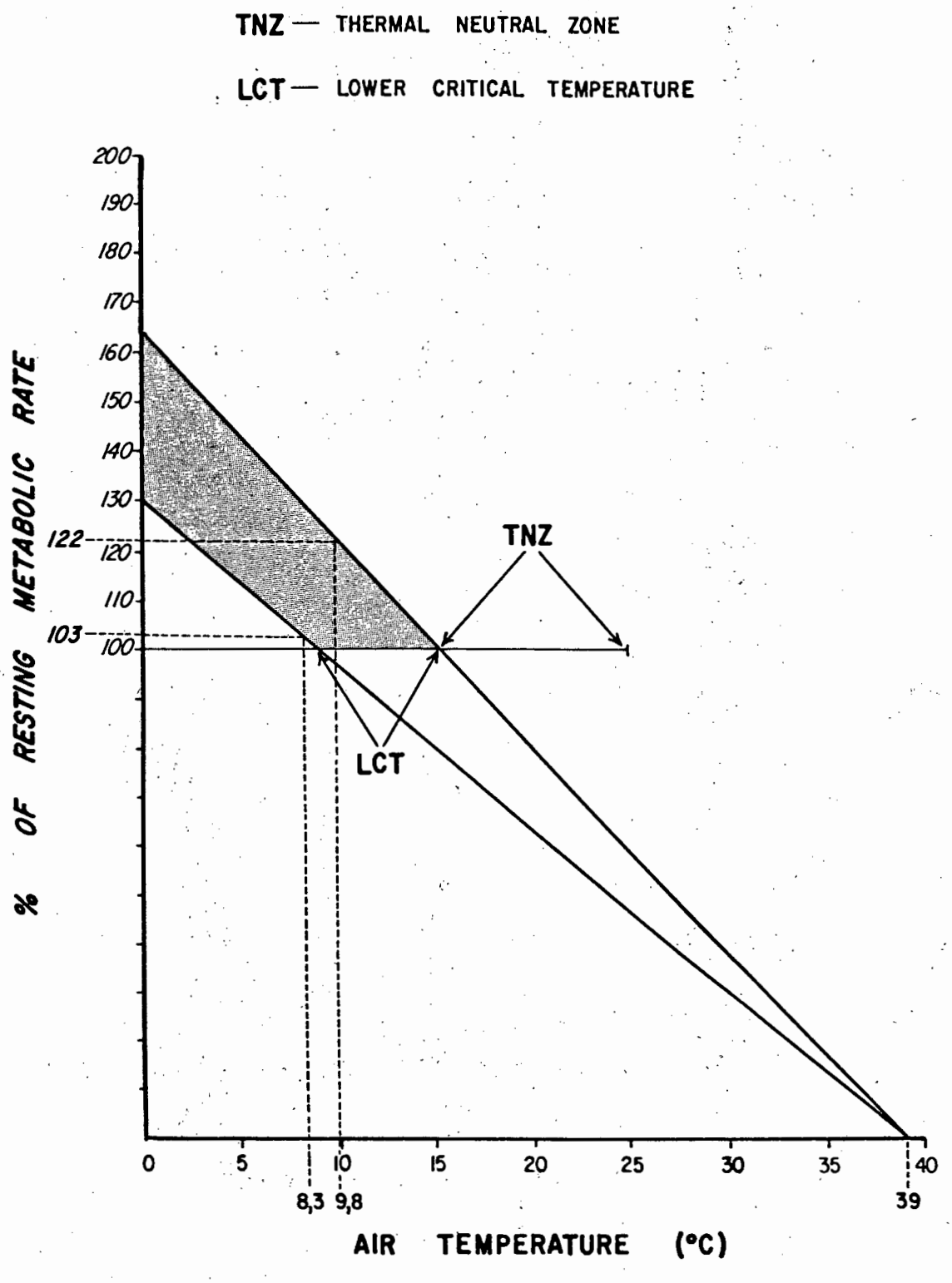

Fig. 5.1 : Relationship between mean minimum air temperature and increment over resting metabolic rate in wildebeest for maintenance of homeothermy at two critically low temperatures.

Table 5.9 : Amount of time in one year when screen temperature at Etosha decreased below two critical thermal parameters for wildebeest

Date (June 1977 to May 1978)	Thermal parameters (No. of hours <10 °C)	Thermal parameters (No. of hours <15 °C)	Total possible hours	% of total time <10 °C	% of total time <15 °C	Mean minimum monthly temp. (°C)
January	0	4	744	0,0	0,5	17,5
February	0	8	672	0,0	1,2	17,3
March	0	1	744	0,0	0,1	17,3
April	4	130	720	0,6	18,1	12,5
May	37	277	744	5,0	37,2	9,2
June	115	329	720	16,0	45,7	7,2
July	121	334	744	16,3	44,9	7,2
August	31	180	744	4,2	24,2	9,6
September	0	64	720	0,0	8,9	13,0
October	1	24	744	0,1	3,2	16,7
November	0	1	720	0,0	0,1	19,6
December	0	3	744	0,0	0,4	18,2
	$\bar{x}$ = 25,75	$\bar{x}$ = 112,92	Σ = 8760	$\bar{x}$=3,53	$\bar{x}$=15,47	$\bar{x}$ = 13,8

mean minimum temperature of 9,8 ^{o}C using an LCT of 15 ^{o}C provided a 22 % increment over RMR. From these data I calculated the energy required for homeothermy in wildebeest for the period of time when ambient temperatures were below both LCTs (Table 5.10).

These increments over RMR required for homeothermy can be expressed as :

$$RE_h = \frac{Eh}{RMR}$$

where RE_h = increment for maintaining homeothermy above a given thermal parameter

Eh = energy cost of homeothermy in a particular class of wildebeest ($kcal.day^{-1}$)

Based on the two LCTs used (10 ^{o}C and 15 ^{o}C), the RE_h is 0,03 and 0,22 respectively (Fig. 5.1).

These coefficients differ markedly from animals with a higher LCT. For instance, in a controlled experiment with a 130 kg eland, Taylor and Lyman (1967) found that the LCT was approximately 20 ^{o}C. The slope they extrapolated to obtain an increment over RMR(RE_h) due to homeothermy gives values of 0,55 and 0,60 at ambient

Table 5.10 : Yearly energy budget for homeothermy in wildebeest at Etosha during 1977/78, applying two critically low thermal parameters

Sex-age and social class	RMR ($kcal.day^{-1}$)	Homeothermic increment over RMR ($kcal.day^{-1}$)		Energy required for homeothermy above LCT for one year (kcal)	
		3 % ($\bar{x} < 10\ ^{o}C = 8,3$)	22 % ($\bar{x} < 15\ ^{o}C = 9,8$)	($\bar{x} < 10\ ^{o}C$ = 3,53 % x 365	($\bar{x} < 15\ ^{o}C$ = 15,47 % x 365
Calf (0-1 year)	1 602,44	48,07	352,54	619,36	19 907,93
Immature & sub-adult cow (1-3 years)	3 075,01	92,25	676,50	1 188,60	38 201,96
Immature & sub-adult bull (1-3 years)	3 375,25	101,26	742,56	1 304,68	41 932,36
Adult cow	3 989,94	119,70	877,79	1 542,27	49 568,80
Adult bull	4 336,56	130,10	954,04	1 676,27	53 874,64

temperatures of 8 °C and 10 °C respectively. If, however, an LCT of 20 °C were to apply to wildebeest, the RE_h values at these ambient temperatures would be 0,53 and 0,58 respectively.

For an estimation of energy required for homeothermy on a yearly basis, it was necessary to consider the percentage of the year when temperatures were below the two critical thermal parameters selected for the purpose of this exercise. During the sampling period of one year, the temperature remained below 10 °C for an equivalent of 12,89 days and below 15 °C for an equivalent of 56,47 days. Applying these values to the daily homeothermic energy requirement given in Table 5.10, corresponding yearly energy requirements were estimated for each major age and sex class.

The total energy calculated for homeothermy in wildebeest at Etosha, on a yearly basis, differed greatly between the two hypothetical LCTs of 10 °C and 15 °C. For example, the difference of 5 °C in the two LCT levels applied here becomes magnified by a factor of 4,38 when the frequency of their occurrence is taken into account (3,58 % and 15,47 % respectively). This difference is further increased by the much higher RE_h of 0,22 which exists at the 15 °C level of LCT. At an LCT of 10 °C,

RE_h is only 0,03. Consequently, if LCT in wildebeest is 15 ^{o}C, the yearly energy for homeothermy at Etosha is 32 times greater than if LCT in wildebeest is 10 ^{o}C. Moreover, in view of Taylor and Lyman's (1967) findings with eland, it seems unlikely that wildebeest would exhibit an LCT as low as 10 ^{o}C in spite of their dark coat colour. Considering all evidence, I have therefore selected 15 ^{o}C as the critical lower temperature for estimating the homeothermic energy budget in wildebeest. It is, however, conceded that this estimate is only approximate in view of the complex physical factors, such as wind speed, surface area and radiation intensity, which are involved in thermoregulation of wild ungulates. Moreover, in all age and sex classes, an increment over RMR due to activity, fell within the range of 1,2 to 1,4. Therefore if we consider an increment of 0,22 as being a fair estimate of metabolic increment for homeothermy, then it would appear as if the heat production for normal activity would provide sufficient energy for homeothermy simultaneously. Nevertheless, in order to provide a maximum estimate of energy requirements for the total population energy budget, I have included this estimate as well.

5.3.7 Comparison of Energy Budgets in Five Major Age-Sex and Social Classes

The energy requirements for existence in free-ranging

wildebeest at Etosha have been compared between five major age-sex and social classes (Fig. 5.2).

5.3.7.1 Maintenance and Activity

Immature and sub-adult bulls had the highest increment over RMR (1,36) and this was due to the greater amount of time they spent in grazing and foraging (Table 5.4). The RE_{ma} in adult bulls was only slightly lower (1,34). Their energy usage was primarily for patrolling and defence of territory and this was reflected in the relatively high percentage of time they spent in walking and social encounters (Table 5.6). Immature and sub-adult cows were fractionally above adult cows in RE_{ma} (1,30 : 1,29), also reflected by their higher rate of grazing and movement (Tables 5.3 and 5.5). Calves were least active (Table 5.2) and consequently closer to RMR than any other class of wildebeest. Their RE_{ma} of 1,20 reflected a high percentage of resting (67,88 %) which they were able to afford at the expense of grazing, being partly dependent on highly nutritive milk.

5.3.7.2 Growth

This energy demand was only studied in wildebeest below three years of age. However, adult wildebeest bulls may

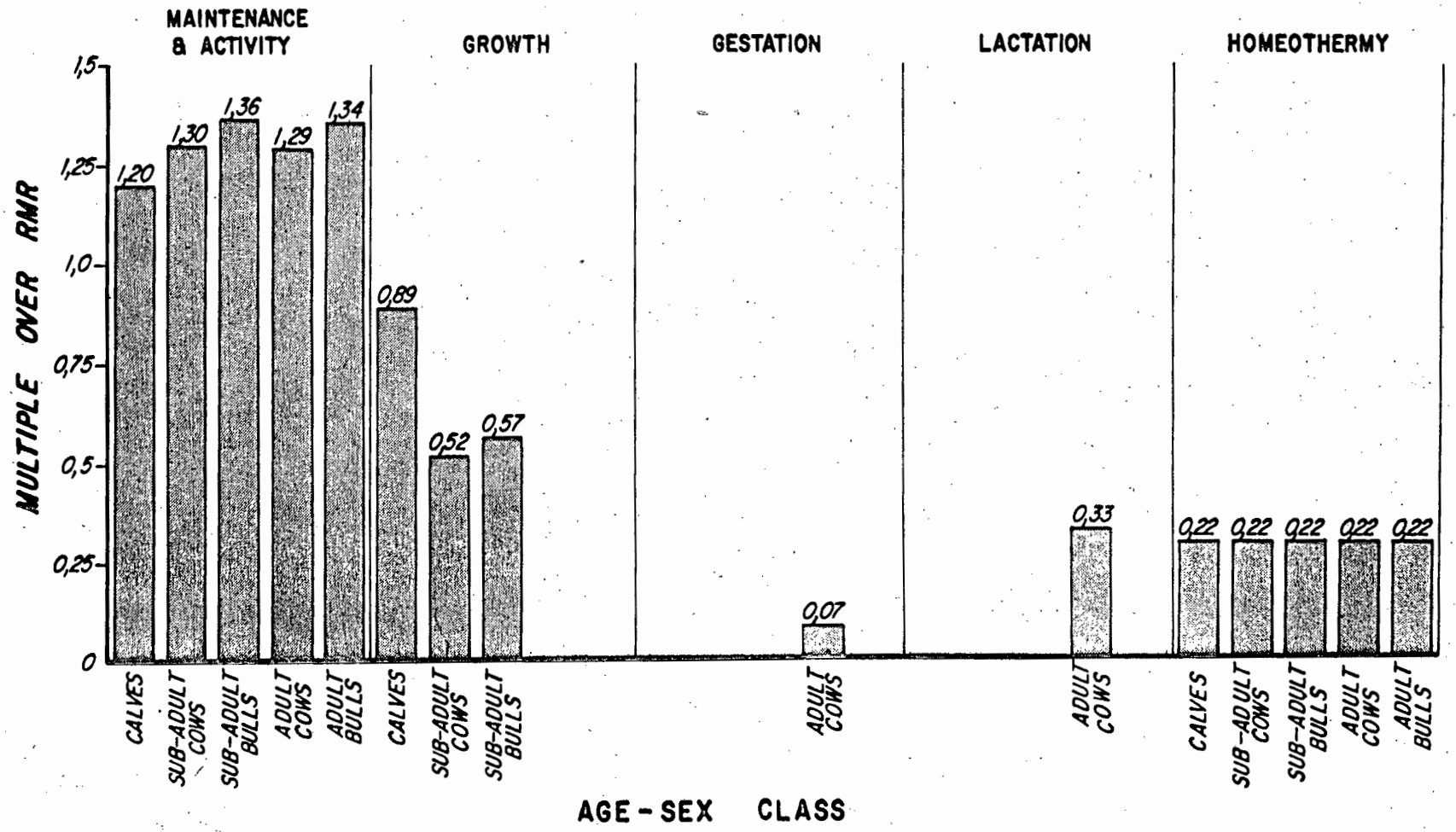

Fig. 5.2 : Comparison of critical life processes expressed as increments over resting metabolic rate in five major age-sex classes of wildebeest at Etosha (1977-78)

continue to increase in body mass up to the age of six years, before reaching the asymptotic value (Attwell, 1977). If this pattern also applies at Etosha, then an RE_g value would exist for adult bulls. However, because of insufficient data for adult bulls, it has been omitted from the present exercise. Similarly, in adult cows, it may take up to six years to reach the asymptote of body mass (Braack, 1973) although Attwell (1977) found that cows attain this value at three years of age. Consequently, adult cows were also not considered for this estimate.

Predictably, calves had the highest RE_g value (0,89). However, they spent only 19,5 % of their time grazing, compared to the overall mean of 32,0 % recorded for wildebeest at Etosha (Section 4). Immature and sub-adult bulls had a higher RE_g value (0,57) than immature and sub-adult cows (0,52). This was due to their far greater increase in body mass between the ages of one and three years (125 kg) than cows during the same period (76 kg) (Table 5.7).

5.3.7.3 Gestation and Lactation

Since only adult cows were involved in these estimates, they can be treated as a special component of the

wildebeest energy budget. Moen (1973) emphasises :

> "The additional energy requirement due to gestation remains small from conception through the first two-thirds of the gestation period. The last one-third of pregnancy is marked by accelerated growth of the foetus, and the energy increment increases. The increase is logarithmic . . . "

In contrast the daily milk production in ungulates follows a typical parabolic curve as the calf increases in body mass and then later becomes less dependent on milk (Moen, 1973). While gestation seldom varies to any large extent from 260 days per annum in wildebeest, lactation varies considerably depending on calf mortality and other factors. As I have observed yearling calves to suckle, it may be that the lactation process never completely ceases in some pregnant, adult cows. Gestation and lactation may, as a result, occur simultaneously for about 70 % of the year, but they never reach a peak increment over RMR simultaneously.

5.3.7.4 Homeothermy

The calculated value of 0,22 was applied to all five major classes of wildebeest, although it will probably vary considerably around this value. In addition, only the lower critical temperature for the maintenance of

homeothermy was considered and energy would also be required for thermal panting above the upper critical temperature. The increase would, however, be slight. Nevertheless, the RE_h value given is likely to be a minimum if the high air temperature and solar radiation at Etosha are taken into account. The compensatory influence of heat increment due to activity has also been considered (Section 5.3.6).

5.3.7.5 Total and Mean Increments over RMR in Wildebeest

In Fig. 5.3 I have illustrated the total increment of energy required above RMR for five major classes of wildebeest. In the case of adult cows the dotted line indicates the energy level if pregnancy and lactation are not involved.

It appears that the growth increment in calves imposed the greatest total energy demand on this age class, calculated on a yearly basis. Immature and sub-adult bulls had the second highest energy requirement because of their high rate of activity in grazing and foraging. Immature and sub-adult cows had a lower level of total energy requirement, which was in keeping with the grazing advantages they enjoyed in a mixed herd (Section 4.3). It is interesting to note that the total grazing time of adult cows (36,34 %, Table 5.5) was considerably lower than that of immature and sub-adult bulls (44,28 %, Table 5.4). Moreover, the energy demands

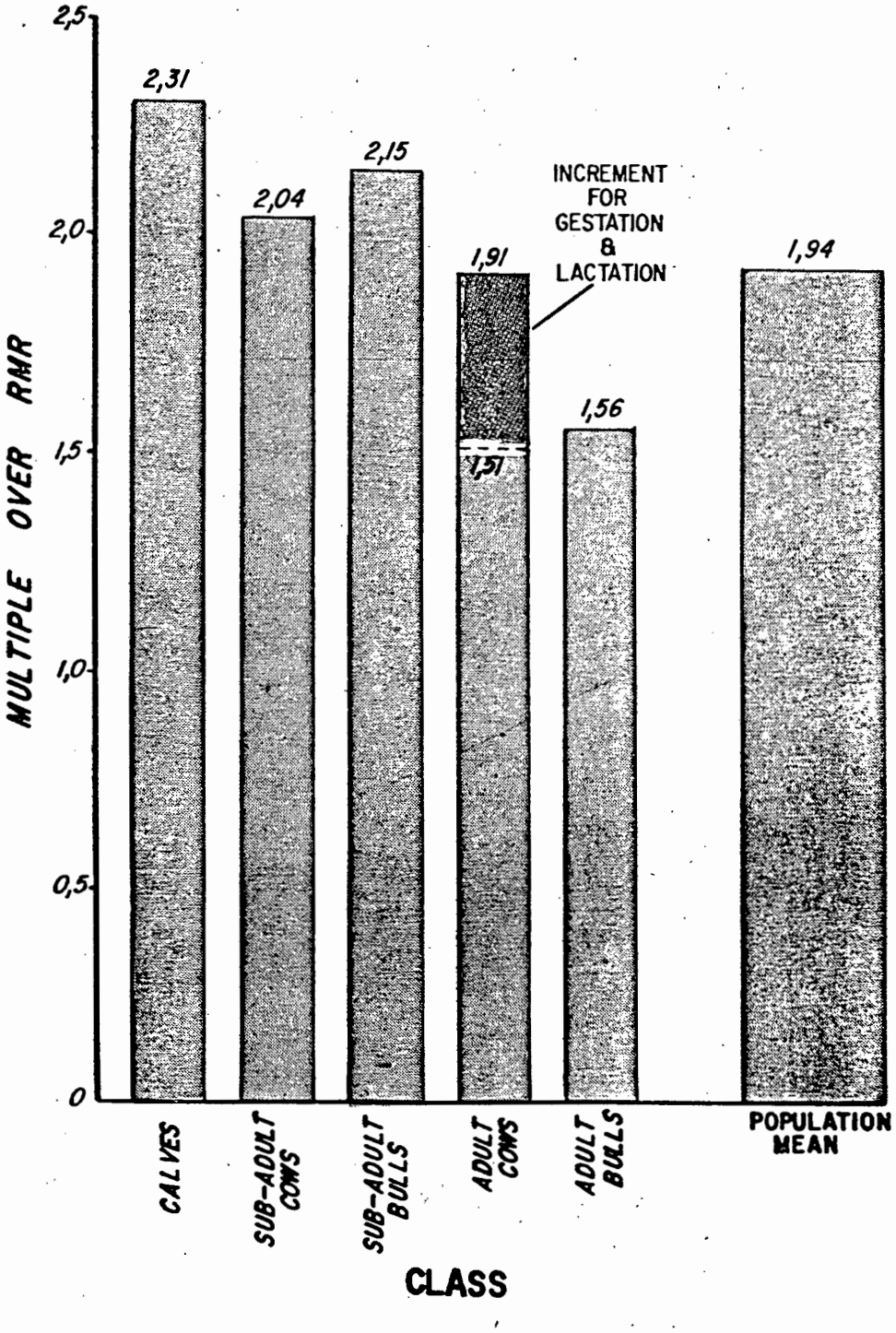

Fig. 5.3 : Comparison of increments over resting metabolic rate for some critical aspects of free existence in five major age-sex classes of wildebeest at Etosha (1977-78).

in adult cows are considerably lower than for immature and sub-adult bulls. This may give quantitative support to the hypothesis advanced by Estes (1966) that cows occupy the best grazing areas, while the bull herds, which include these growing bulls, are relegated to areas of inferior grazing (see also Section 4.3 of this thesis). Adult bulls, and adult cows which are not reproducing, have the lowest relative energy demands. Nevertheless, the increment over RMR in adult bulls will vary around this parameter, depending upon their social status.

A mean increment over RMR for the wildebeest population has also been indicated in Fig. 5.3. This value of 1,94 was calculated by multiplying total increment over RMR in each age-sex and social class by the percentage of the population which each class comprised (Table 5.1). The coefficients, in decreasing order of magnitude are : adult, pregnant/ lactating cows (0,57), calves (0,46), adult bulls (0,37), immature and sub-adult cows (0,27), immature and sub-adult bulls (0,22), adult non-pregnant/non-lactating cows (0,05).

I wish to emphasize that these calculations must be regarded as a first approximation of the energy required for free-ranging wildebeest at Etosha. Insufficient quantitative data exist for the determination of all parameters of free existence. For instance, the energy cost of rumination,

which has been given as an increment of 1,26 over RMR for a 100 kg animal (Moen, 1973), could not be calculated for wildebeest. Similarly, I was unable to give any meaningful estimate of the energy required for heat loss above the upper critical body temperature. This is, however, a very small error, and is compensated by the fact that I have probably overestimated the requirements for homeothermy (Section 5.3.6).

The main conclusion emerging from the present study is that the metabolic cost of free existence in wildebeest appears to be similar to other wild ungulates. For instance, in a free-ranging 60 kg deer the metabolic cost has been estimated by Moen (1973) to range from 1,42 for maintenance and activity to 2,3 when lactating with two fawns. He consequently holds that the multiple of RMR seldom exceeds 2,0 in deer. However, to my knowledge, the present study is the first attempt to quantitatively translate the activity patterns of a discrete population of free-ranging African ungulates to an energy budget. If it is considered that my estimate of 1,94 for increment over RMR in wildebeest does not include the requirements for rumination or parasitism cost, then this first approximation may be considered conservative. Nevertheless, the activity of wildebeest on moonless nights has not yet been accurately monitored and there may be a decrease in activity during

these periods (Section 4.3.6.4). This decrease may compensate to some extent for the increase due to rumination, parasitism and other as yet unmeasured energy parameters. Considering all these factors, it seems reasonable to accept that the energy cost of free existence to wildebeest at Etosha approximates 2,0 times their RMR.

Furthermore, Rogerson (1968) has found in controlled experiments that wildebeest may have a far greater RMR than the presently accepted standard. He calculated a resting metabolic rate of $104,3W^{0,73}$ for wildebeest, compared to the internationally recognised formula of $70W^{0,75}$ (National Research Council, 1966). If the figure calculated by Rogerson (1968) is applied to the mean body mass of wildebeest at Etosha (181,11 kg) then RMR is 4 640,69 $kcal.day^{-1}$. This is 36 % higher than the mean RMR of 3 415,22 $kcal.day^{-1}$, which was found in this study.

To summarise : available data suggest that the energy cost of free-existence to wildebeest at Etosha is comparable to other wild ungulates. The most vulnerable components of the population are the growing animals and adult, pregnant/lactating cows. The high energy demands imposed on calves can be ascribed to the cost of growth. Advanced precocity in wildebeest calves is a well-observed phenomenon (Estes, 1966; Watson, 1967) but the accompanying

energy demand on pregnant cows is unknown. Adult cows also comprise the largest segment, namely 33 % of the population, and so their contribution towards the total energy budget is relatively very high. Adult bulls, on the other hand, have a low total energy demand, although they form 24 % of the population. Only a mean value for adult bulls was estimated for the purpose of calculating a total energy budget. The energy required by a rutting bull will certainly be higher, and the data for this calculation are available from my study. Similarly, the data potential which has been accumulated during the present exercise will allow for a more refined analysis of energy demand on a seasonal basis in the major classes of wildebeest at a future date. For instance, the cost of gestation and/or lactation can be assessed in terms of time of the year. Finally, the above changing costs can be related to the quality of the grazing on a seasonal basis.

5.3.8 Population Energy Budget

To calculate the total energy budget of Etosha's wildebeest population for one year, the sum of the energy requirements in each individual was determined as given in Appendix 9. The individual totals were then multiplied by the number of animals in each class to obtain the total amount of energy required in one year per class. To facilitate reference

to formulae used in earlier discussion (Sections 5.3.2 to 5.3.7), energy requirements have been expressed in megacalories (Mcal) as well as megajoules (MJ) in Table 5.11. In the case of lactating cows, energy requirements on a yearly basis have not been made on the assumption that each cow giving birth will keep her calf for a full year. Instead, I have applied the formula for determination of energy required in the milk (Section 5.2.2.10), to a decreasing number of calves at intervals of three months, six months and nine months after birth. To estimate the number of calves surviving after three months, I assumed a monthly calf loss of 42 after all births for the season had occurred. This figure was based on the difference between total number of pregnant cows and number of calves counted six months after the calving season.

Thus : 748 - 498 = 250 calves lost in six months

$\bar{x}$ = 41,67 calves lost per month

Therefore : 748 - (41,67 x 3 months) = 622 calves survived to three months of age

Similarly : 498 = number of calves counted at six months of age

and

325 = number of yearlings counted

Thus : $\bar{x}$ = 28,83 calves per month

= 412 calves survived to nine months of age.

Table 5.11 : Population energy budget for wildebeest at Etosha during one year (1977/78)

Age and sex class	Percentage of population	Population energy budget	
		(Mcal.year^{-1})	(MJ.year^{-1})
Calves (0-1 year)	20	618 682	2 588 567
Immature and sub-adult cows (1-3 years)	13	677 369	2 834 113
Immature and sub-adult bulls (1-3 years)	10	612 350	2 562 072
Adult, non-reproductive cows	3	145 038	606 838
Adult, reproductive cows	30	1 745 736	7 304 159
Adult bulls	24	1 298 155	5 431 479
Totals	100	5 097 330	21 327 228

Appropriate modifications were made to other parameters of the formula, namely, body mass of calves and the rumen development factor (Section 5.3.5). Consequently, at three months of age a body mass of 44 kg and an RD factor of 0,75 was applied. Similarly, at six months of age, the body mass was taken to be 65 kg and the RD factor to be 0,5. Finally, at nine months of age, body mass was 86 kg and the RD factor was 0,25.

Based on these criteria, energy estimated to be present in the milk of each cow was :

1 197,38 $kcal.day^{-1}$ for calves aged 3 months,
727,64 $kcal.day^{-1}$ for calves aged 6 months, and
448,82 $kcal.day^{-1}$ for calves aged 9 months.

Each of these estimates was then multiplied by the number of calves surviving at the respective intervals and by the number of days applicable to each interval. The resultant sub-totals were then summed and multiplied by a factor of 1,6 to give the energy required by the cows to produce the milk (Crampton and Harris, 1969).

The first approximation of the population energy budget of 2 493 free-ranging wildebeest at Etosha during 1977/78 was 21 327 228 $MJ.year^{-1}$, or approximately 21,3 terajoules (TJ).

An estimation of the mean energy requirement per wildebeest, taking into account the percentage which each class contributed to the population (Section 5.2.3) was 8 555 $MJ.year^{-1}$, or approximately 8,5 gigajoules (GJ). The relative requirements of each class of wildebeest for the various categories of energy, and the relative contribution which each class made to the population energy budget, could also be calculated from the preceding exercise. These data are shown in Table 5.12.

The population energy budget put forward here is naturally not rigid, but exists in a state of continual flux as the demography and the parameters encountered by the free-ranging population change dynamically. Although the energy budget of a wild ungulate species, such as wildebeest, must for the present remain an approximation, it is based on quantitative data. The energetic cost of free existence can subsequently be balanced against energy supply of the food source, thereby providing a sound basis for estimating habitat utilisation.

5.4 SUMMARY

5.4.1

This study was designed to make a first approximation of

Table 5.12 : A comparison of the relative energy requirements of various classes within the wildebeest population at Etosha (1977 - 78)

Age-sex & social class	Energy category	Relative requirement (%)	Relative contribution to population energy budget (%)
Calves (0-1 year)	Maintenance & activity	7,0	12
	Growth	5,0	
	Homeothermy	0,2	
Immature & sub-adult cows (1-3 years)	Maintenance & activity	9,0	13
	Growth	4,0	
	Homeothermy	0,2	
Immature & sub-adult bulls (1-3 years)	Maintenance & activity	8,0	11
	Growth	3,0	
	Homeothermy	0,2	
Adult, non-reproductive cows	Maintenance & activity	3,0	3
	Homeothermy	0,1	
Adult, reproductive cows	Maintenance & activity	28,0	35
	Gestation	1,0	
	Lactation	5,0	
	Homeothermy	0,7	
Adult bulls	Maintenance & activity	25,0	26
	Homeothermy	0,6	
		Σ = 100	Σ = 100

the energy budget of Etosha's wildebeest by allocating energy values to their various life processes. Energy requirements were calculated for each of the five major age-sex and social classes.

5.4.2

Dissimilarities in the diurnal and nocturnal activities of wildebeest were considered by application of a correction factor for energy required during a 24-hour cycle of activity.

5.4.3

The increment in energy expenditure for each of 12 specific activity categories was applied to the resting metabolic rate (RMR) for a 24-hour activity cycle. Thereby an expression of the relative cost of each activity to wildebeest was obtained.

5.4.4

The categories of energy cost, which were estimated in the population, were for maintenance and activity, growth, gestation, lactation, and some aspects of homeothermy. Mean increments over RMR for the different age and sex classes were 1,30 for maintenance and activity, 0,66 for growth, 0,07 for gestation, 0,33 for lactation, and 0,22 for homeothermy.

5.4.5

The coefficients of increase in energy usage were subsequently compared between five major age-sex and social classes. Calves exhibited the highest coefficient (2,31 RMR), with immature and sub-adult bulls and cows slightly lower (2,15 RMR and 2,04 RMR respectively). Reproductive cows had a coefficient of 1,91 RMR. The lowest coefficients were found in adult bulls (1,56 RMR) and non-pregnant/dry cows (1,51 RMR).

5.4.6

Mean increment over RMR for the wildebeest population, taking into account the relative contribution of each major age-sex and social class, was estimated to be 1,94. This was very similar to an estimate obtained for free-ranging white-tailed deer which approximated 1,8 (Moen, 1973). Nevertheless, the estimate for wildebeest may still be conservative, since not all aspects of energy expenditure were investigated. An increment of 2,0 times RMR was considered to be a realistic coefficient for free existence in Etosha's wildebeest.

5.4.7

A yearly population energy budget revealed that the

estimated 2 493 free-ranging wildebeest at Etosha required 21,3 terajoules. This was equivalent to 8,5 gigajoules for an individual wildebeest.

5.4.8

The data collected during this study suggest that the energy cost of free existence to wildebeest at Etosha is similar to other wild ungulates. Growing animals and reproductive cows were the most vulnerable components of the population in this regard and exhibited the same energy requirements as previously studied ungulates. This was probably due to the high energy content of wildebeest milk, the precocity of calves and their swift growth.

Section 6

PROTEIN BUDGET

6.1 INTRODUCTION AND TERMINOLOGY

Protein is the principal constituent of the organs and soft structures of an animal's body, requiring a liberal and continuous supply for growth and repair of tissue (Maynard and Loosli, 1962). Thus the protein budget of animals such as wildebeest is a very important consideration in evaluating their nutritional status. As in the case of the wildebeest's energy budget, my interest in constructing a protein budget for the species was to test whether the grasslands of Etosha produced sufficient crude protein on a seasonal basis to meet the demands made by a free-living population. The protein take-off by grass eating competitors of wildebeest will be discussed separately (Section 8).

My approach in this investigation was to calculate the protein requirements of an individual wildebeest for the basic life processes of maintenance, growth, gestation and lactation, as described by Moen (1973). Thereafter, the protein budget of the population was approximated by making

allowance for the differences between the requirements of the various age-sex and social classes of wildebeest, and by taking into account the seasonal changes occurring in the population. Because field data for protein requirements in wild ungulates are largely unavailable (Moen, 1973), I applied data for domestic ungulates, such as cattle. This protein budget for wildebeest must therefore necessarily be regarded as a first approximation which may be refined as techniques for measuring the nutritional needs of wild ruminants improve.

The terms to be used in this discussion were taken from the Agricultural Research Council (1965) and Moen (1973). They are :

(a) Endogenous urinary nitrogen (EUN)

The nitrogen excreted in the urine, which is derived from the catabolism of body tissue.

(b) Metabolic faecal nitrogen (MFN)

The nitrogen loss contained in the faeces due to mechanical abrasion of the digestive tract by food, plus spent enzymes and bacterial residues.

(c) Retained nitrogen (RN)

The nitrogen used in the body proteins for tissue deposition, hair growth, gestation and lactation.

6.2 METHODS

6.2.1 Calculation of nitrogen requirements

6.2.1.1 Maintenance

For a first approximation of the nitrogen required for replacement of catabolised body tissue in wildebeest, I applied the formula proposed by Moen (1973) which is based on earlier findings of Crampton and Harris (1969) and Brody (1945) :

$$Q_{eun} = \frac{2 \times 70(W_{kg}^{0,75})}{1000}$$

where Q_{eun} = endogenous urinary nitrogen in g. day^{-1}

2 = ratio of N in mg/kcal in the equation for RMR = (N_{mg}/kcal)

W_{kg} = wildebeest live body mass in kg

To estimate the nitrogen required to compensate for losses in metabolic faecal nitrogen (MFN), the formula suggested

by Moen (1973) was used :

$$Q_{mfn} = cF_{kg}/6,25$$

where Q_{mfn} = metabolic faecal nitrogen in g. day^{-1}

c = 5 for forage diets; 2,5 for milk diets; intermediate values for milk and forage diets

F_{kg} = wildebeest food DM intake in kg. day^{-1}

6.2.1.2 Growth

Firstly, to estimate nitrogen requirement for production of new body tissue, I referred to the retained nitrogen (RN) range of 2,40 - 3,50 % of the daily gain in body mass (ARC, 1965). Lower values were used in the case of sub-adult wildebeest, which deposit less protein, and the highest value was used for calves, which exhibit a greater growth in protein tissue. Values intermediate to these two extremes were used for immature classes. Thus, based on the mean daily gain in body mass (Section 5.3 : Table 5.7) the nitrogen values allocated were : immature cows (3,16 %), immature bulls (3,28 %), sub-adult cows (2,61 %), sub-adult bulls (3,01 %). Based on the equation proposed by Moen (1973), this is expressed as :

$$Q_{ng} = RN \Delta W_{kg}/100$$

where Q_{ng} = quantity of nitrogen required for daily gain in g. day^{-1}

RN = retained nitrogen value for the age-sex class of wildebeest measured

ΔW_{kg} = gain in body mass in kg. day^{-1}

Secondly, to estimate the nitrogen required to produce hair, I assumed that nitrogen depletion caused by hair and scurf loss in wildebeest would be somewhat lower than that reported for domestic cattle (ARC, 1965) because wildebeest have a shorter pelage. Consequently, the equation used by Moen (1973) was modified to include a correction factor of 0,6. Thus :

$$Q_{nh} = (0{,}02\ W_{kg}^{\ 0{,}75})\ (0{,}6)$$

where Q_{nh} = quantity of nitrogen required for hair growth in g. day^{-1}

W_{kg} = live body mass of wildebeest in kg

6.2.1.3 Gestation

The predictable increase in RN as pregnancy progresses, increases daily in a logarithmic manner (Moen, 1973). To make a first approximation of the nitrogen requirements in pregnant wildebeest, I considered the RN in the foetus, placenta, uterus and amniotic fluids of domestic cows (ARC,

1965). Then, applying an appropriate conversion factor for expressing the equivalent time in the gestation period of wildebeest, the modified equation, based on that given by Moen (1973) will be :

$$Q_{np} = \frac{e^{a + b(t_d/c)} W_{kg}}{6,25}$$

where Q_{np} = nitrogen requirements on the particular single day selected within the gestation period in $g.day^{-1}.kg$ foetus mass at term

e = natural logarithm

$a + b$ = constants, using domestic cattle as a baseline

t_d = number of days pregnant, namely any single day selected within the gestation period

c = conversion factor for gestation time of wildebeest

W_{kg} = birth mass of standard (domestic calf) in kg

The constants (a + b) in the above equation were taken as (-3,1206 + 0,0298) respectively (Moen, 1973), whilst the conversion factor for wildebeest gestation time 260/280 days = 0,92857 (Section 5.3.4).

To integrate the above equation for the purpose of calculating the total area under the curve of the exponential increase in nitrogen required for gestation in wild ruminants (Moen, 1973) then :

using the symbol d to replace $^{b}/_{c}$

and integrating :

$$\int_{o}^{t} Q.dt = \frac{\int_{o}^{t} e^{a + dt/w}.dt}{6,25}$$

$$= \frac{\frac{c.e^{a}}{W.b}(e^{bt/c} - 1)}{6,25}$$

where c = 0,92587

e = 2,718

a = -3,1206

b = 0,0298

W = 45

t = total gestation period for wildebeest
= 260 days

6.2.1.4 Lactation

Because lactation requirements in free-ranging wildebeest calves have not been measured, I used a regression equation for white-tailed deer (Moen, 1973) :

$$\% \text{ MD} = 113{,}6 - 4{,}5\ W_{kg}$$

which has been discussed fully under energy estimates for lactation (Section 5.3.5). Then, assuming that RN for lactation includes nitrogen contained in the milk plus the nitrogen required by the cow to produce this milk, the total nitrogen requirement (Moen, 1973) is :

$$Q_{nl} = \frac{(Q_{mp})\ (N\ \%)(I_{mp})}{100}$$

where Q_{nl} = nitrogen required for lactation in $g.day^{-1}$

Q_{mp} = quantity of milk produced in $g.day^{-1}$

N % = percent nitrogen in milk

I_{mp} = metabolic increment for milk production

The Q_{mp} value was calculated from the equation proposed by Moen (1973) :

$$Q_{mp} = \frac{(W_{kg})\ (MD)\ (Q_{pf}/6{,}25)}{(NF)\ (P_c)}$$

where W_{kg} = mean seasonal body mass of a wildebeest calf in kg

MD = milk dependence on a seasonal basis

Q_{pf} = quantity of protein required by a wildebeest calf in $g.kg^{-1}.day^{-1}$

6,25 = conversion factor to reduce Q_{pf} to nitrogen

NF = nitrogen fraction in wildebeest milk

P_c = net protein coefficient for milk

and W_{kg} = 33 kg at the midpoint for lactation in the wet, hot season (105 days of lactation : from 15 January to 30 April)

= 61 kg at the midpoint for lactation in the dry, cold season (123 days of lactation : from 1 May to 31 August)

= 82 kg at the midpoint for lactation in the dry, hot season (62 days of lactation : from 1 September ending 31 October)

(Seasonal W_{kg} was extrapolated from daily gain in live mass of calves from birth to one year, namely 0,230 kg : Section 5.3, Table 5.7, and the lactation period was taken at 290 days.)

MD = 0,75 in the wet, hot season

= 0,5 in the dry, cold season

= 0,25 in the dry, hot season

(based on the formula discussed in Section 5.3.8)

Q_{pf} = 3,3 (based on the range 3,3 - 6,6 given by Moen (1973) and considering the mean daily increment of 0,230 kg in wildebeest calf mass : Table 5.7)

NF = 0,00907 (based on mean protein content of 5,67 % in wildebeest milk : Section 7.3, Table 7.16)

P_c = 0,85 (Brody, 1945)

The calculation of Q_{nl} requires that the nitrogen percentage be known. I used a value of 0,9072 % calculated from a mean protein content of 5,67 % for wildebeest. Lastly, the nitrogen requirement by a wildebeest cow to produce the milk (I_{mp}) was estimated by multiplying the percentage nitrogen in the milk by a factor of 1,38 based on data in Crampton and Harris (1969). This calculation of I_{mp} can be regarded as an "overhead" expense in the nitrogen requirements for lactation (Moen, 1973).

6.2.1.5 Parasites

As in the case of the energy budget, I could not trace any quantitative data for protein cost of parasites or pathogens to an ungulate (Section 5.2.2.10). However, the level of parasitism in Etosha's wildebeest is very low (Section 10) and for the purpose of this study it was ignored.

6.2.2 Calculation of an Individual Protein Budget

The protein budget of an individual wildebeest was based on the amount of nitrogen metabolised by the body. An equation for this purpose, modified from that proposed by Moen (1973), was used for Etosha's wildebeest :

$$PR = \Sigma(Q_{eun} + Q_{mfn} + Q_{ng} + Q_{nh} + Q_{np} + Q_{nl})(6,25)$$

where PR = protein required in $g.kg^{-1}.day^{-1}$

Q_{eun} = daily EUN

Q_{mfn} = daily MFN

Q_{ng} = daily nitrogen required for gain

Q_{nh} = daily nitrogen required for hair growth

Q_{np} = daily nitrogen required for pregnancy

Q_{nl} = daily nitrogen required for lactation

6,25 = protein : nitrogen ratio in body tissue

6.2.3 Calculation of the Population's Protein Budget

A first approximation of the wildebeest population's protein budget at Etosha was attempted on a seasonal basis

for a period of one year. To achieve this, I used the population structure which existed in 1977/78 (Section 5.3, Table 5.1), applying the seasonal variations which occurred in body mass and number of individuals (Section 7.3, Appendix 20). The protein requirements for each major age-sex and social class were then computed on a seasonal basis.

6.3 RESULTS AND DISCUSSION

The detailed nitrogen requirements for 10 major age-sex and social classes of wildebeest are shown on a seasonal basis in Appendix 10 and summarised in Table 6.1. Maintenance, growth, gestation and lactation for the individual have been taken into account, to give a daily total requirement. For seasonal data on mean body mass and DM food intake, I referred to Section 7.3.9, Appendix 20.

6.3.1 Nitrogen Requirements for Maintenance

As expected EUN values were considerably higher than MFN values. This was especially apparent in the case of rapidly growing calves. The changing MFN values are a reflection of the seasonally changing milk : forage ratio

Table 6.1: Estimation of total daily nitrogen requirement in individual wildebeest at Etosha, on a seasonal basis (1978)

Age - sex and social class	Seasonal nitrogen requirements ($g.day^{-1}$)		
	Wet, hot (Jan. to April)	Dry, cold (May to Aug.)	Dry, hot (Sept. to Dec.)
Calf (0-1 yr)	10,61	12,10	13,81
Immature cow (1-2 yrs)	13,24	13,26	14,18
Immature bull (1-2 yrs)	14,99	15,28	16,48
Sub-adult cow (2-3 yrs)	12,40	11,34	11,63
Sub-adult bull (2-3 yrs)	16,50	15,81	16,59
Adult, non-pregnant cow	11,96	10,50	10,26
Adult, lactating & pregnant cow	34,59	36,97	23,99
Lone, territorial bull	14,60	12,74	12,74
Adult bull in mixed herd	15,07	13,15	13,15
Adult bull in bachelor herd	15,55	13,55	13,55

of calves. For instance, protein loss during the wet, hot season was 2,91 $g.kg^{-1}.day^{-1}$ in newly born calves. Older calves, in the dry, cold season, consumed more forage, which resulted in increased mechanical abrasion of the digestive tract and therefore greater protein loss (3,74 $g.kg^{-1}$). For the dry, hot season, protein loss was even greater (4,58 $g.kg^{-1}.day^{-1}$).

6.3.2 Nitrogen Requirements for Growth

Predictably, calves had the highest relative nitrogen requirement for growth, followed by immature and sub-adult bulls which gained body mass more rapidly than their female counterparts (Section 5.3, Table 5.7). In all classes of wildebeest, the growth of hair required fractional amounts of nitrogen. However, this parameter has been included to demonstrate that subtle demands of this type did exist in the protein budget.

6.3.3 Nitrogen Requirements for Gestation

At Etosha, wildebeest calving is usually at a peak in mid-January and therefore the nitrogen requirements will be greatest in this period, immediately prior to parturition. Q_{np} is the quantity of nitrogen required for pregnancy in $g.day^{-1}.kg$ foetus mass at term

(Section 6.2.1.3) and was calculated at 20,54 g or 472 g.day^{-1}.foetus^{-1} (20,54 g x 23 kg birth mass). Since no foetuses were available during this study, the findings of Attwell (1977) for increment in wildebeest foetal mass were used. Taking a gestation period of 260 days, commencing at the beginning of May, which is the height of the rut, the birthdate will be mid-January the following year. According to Attwell (1977), foetal mass reaches 1 kg about 123 days after conception. This is the length of the dry, cold season at Etosha and I have assumed a daily mean gain of 0,00813 kg (1,0 kg/123 days) in the foetus. At the midpoint of the season the foetus will measure 0,5 kg (0,00813 kg x 61,5 days) and would require a very small amount of nitrogen (0,003g.day^{-1}, on average). Likewise, foetal mass at the midpoint of the dry, hot season approximated 9,5 kg, which required 3,63 g.day^{-1}. During the wet, hot season the nitrogen requirement for gestation dropped drastically when calculated as a mean for the season (120 days). This was because birth occurred theoretically on 15 January and so the 23 kg foetus required 15,17 g N.day^{-1} x 15/120 = 1,90 g N.day^{-1}. These mean seasonal nitrogen requirements, when multiplied by the gestation period of 260 days, gave an amount of 472 g N, which was the estimated cost of a complete pregnancy in wildebeest.

6.3.4 Nitrogen Requirements for Lactation

The nitrogen content of wildebeest milk (0,9072 %) was lower than that of white-tailed deer (1,76 %, Moen, 1973). Consequently, the quantity of milk needed to satisfy nitrogen requirements in wildebeest calves (Q_{mp}) was relatively higher. This assumption is inherent in the equation for estimating Q_{mp} (Section 6.2.1.4), since NF is accordingly reduced in value. For example, Q_{mp} was 1 694 $g.day^{-1}$ (wet, hot season), 2 089 $g.day^{-1}$ (dry, cold season), and 1 403 $g.day^{-1}$ (dry, hot season). However, in the final formula for calculating nitrogen required for lactation (Q_{nl}), the increased Q_{mp} value was compensated for by the reduction in the value of N. Nonetheless, the nitrogen demand by a lactating wildebeest cow was very high, since the production of milk has been assumed to require 1,38 times the amount of nitrogen contained in the milk. If Q_{nl} is considered for the wet, hot season (18,57 $g.day^{-1}$, Appendix 10), it is interesting to note that 13,46 g N (18,57 g/1,38) would be available in the milk. Furthermore, the calf's requirement was 10,61 $g.day^{-1}$, most of which was supplied by the milk. Assuming that milk production of a wild ruminant is in balance with the requirements of its nursing offspring (Moen, 1973), it was evident from my approximations that a wildebeest cow produced more nitrogen than the calf required. However,

the daily quantity of protein in $g.kg^{-1}$ (Q_{pf}) required by a wildebeest calf is unknown and I have used an arbitrary value of 3,3 $g.kg.day^{-1}$ (Crampton and Harris, 1969). This may be a source of error. Similarly, in the dry, cold season, the wildebeest cow's nitrogen production in the milk was 18,95 $g.day^{-1}$ while the calf's requirement was 12,10 $g.day^{-1}$. In the dry, hot season when lactation ended and the weaned calf's nutrient requirements were met by forage, the milk contained 6,47 g $N.day^{-1}$, whereas the calf's requirement was 13,81 g $N.day^{-1}$. In any event, the above arguments demonstrate that nitrogen requirements for lactation have not been underestimated.

6.3.5 Seasonal Protein Budget of the Individual

To make a first approximation for seasonal protein requirements of the major classes of wildebeest (Appendix 11), a protein : nitrogen coefficient of 6,25 was used (ARC, 1965) and applied to the sums of the daily nitrogen requirements (Appendix 10). Thereafter the seasonal demand was estimated by taking 120 days (wet, hot season), 123 days (dry, cold season), and 122 days (dry, hot season). The results are summarised in Table 6.2.

Table 6.2: Estimate of the seasonal protein budget of the wildebeest population at Etosha (1978)

Age - sex and social class	Seasonal protein requirements (kg)		
	Wet, hot (Jan.to April)	Dry, cold (May to Aug.)	Dry, hot (Sept.to Dec.)
Calves (0-1 yr)	5 396	4 995	4 159
Immature cows (1-2 yrs)	1 579	1 529	1 535
Immature bulls (1-2 yrs)	1 743	1 621	1 508
Sub-adult cows (2-3 yrs)	1 246	1 116	1 082
Sub-adult bulls (2-3 yrs)	1 312	1 142	1 037
Adult, non-pregnant cows	673	605	587
Adult, lactating & pregnant cows	19 405	21 259	13 682
Lone, territorial bulls	1 916	1 469	486
Adult bulls in mixed herds	1 130	1 011	1 003
Adult bulls in bachelor herds	3 779	3 636	4 369
Seasonal totals	38 179	38 383	29 718
Yearly total	106 280		

6.3.6 Comparison of Protein Budgets in 10 Major Age-Sex and Social Classes

The critical parameters of protein demand in free-ranging wildebeest at Etosha were compared between 10 major classes on a mean daily basis for one seasonal year (Fig. 6.1). Adult, reproductive cows had a very high protein demand (199,06 $g.day^{-1}$ per individual). This was due to the processes of gestation and lactation which jointly imposed a continuous demand for protein throughout the year. Sub-adult and immature bulls had the second highest requirement (101,86 and 97,41 $g.day^{-1}$ respectively). Adult bulls in bachelor herds required 88,80 $g.day^{-1}$, those in mixed herds required 86,13 $g.day^{-1}$, while lone, territorial bulls' demand was fractionally lower than immature cows' (83,45 $g.day^{-1}$ as opposed to 84,76 $g.day^{-1}$). Calves (76,14 $g.day^{-1}$), sub-adult cows (73,66 $g.day^{-1}$) and non-reproductive cows (68,12 $g.day^{-1}$) had the lowest protein requirements per individual.

6.3.7 Seasonal Protein Budget of the Population

The population's protein budget was derived directly from the individual's requirement by multiplying by the number of animals in each class (Appendix 11). During the wet, hot season, the population was at its greatest in terms

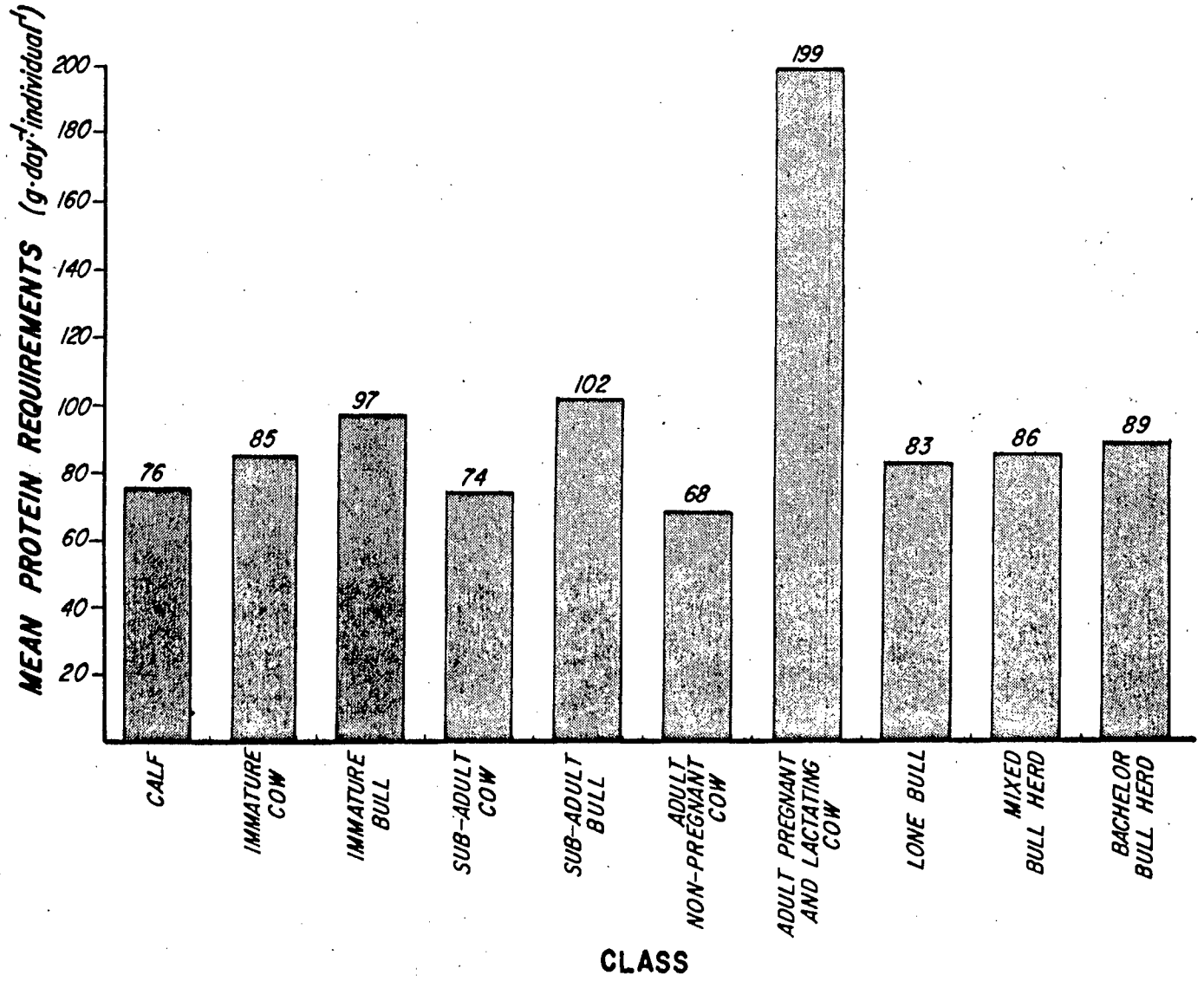

Fig. 6.1 : Mean daily protein requirements in 10 major age-sex classes of wildebeest at Etosha (1978).

of numbers, biomass and growth. Consequently, the demand for protein was high. These three parameters decreased in the dry, cold season, but in the case of reproductive cows whose milk production was at a peak, protein demand increased. The dry, hot season was a period of low numbers and biomass for the population, and pregnant cows also entered a period of decreased protein demand, for, although their foetuses gained logarithmically in mass, their milk production decreased. It is therefore noteworthy that the protein demand by the population appears to have adjusted to the seasonal supply of this critical nutrient. This protein balance will be discussed in Section 8.4.2.

6.3.8 Relative Yearly Protein Demand by Various Classes of the Population

The protein required by each of the 10 major age-sex and social classes of wildebeest, taking into account their relative numerical contribution to the population was calculated. This demand is given in Table 6.3 in decreasing order of magnitude. Thus, reproductive cows required more than half the population's protein need and their calves had the second highest requirement. Together, these two components of the population accounted for 65 % of the protein demand. They would consequently

Table 6.3: Relative yearly protein demand in the wildebeest population at Etosha (1978)

Age - sex and social class	Yearly Protein Requirements	
	Total (kg DM)	Percentage of Total
Adult, lactating and pregnant cows	54 346	51,1
Calves	14 550	13,7
Adult, bachelor herd bulls	12 054	11,3
Immature bulls	4 872	4,6
Immature cows	4 643	4,4
Lone, territorial bulls	3 871	3,6
Sub-adult bulls	3 491	3,3
Sub-adult cows	3 444	3,2
Adult, mixed herd bulls	3 144	3,0
Adult, non-pregnant cows	1 865	1,8
TOTALS	106 280	100

be the most vulnerable if insufficient protein were to be produced by the grasslands of Etosha. The critical position occupied by pregnant and lactating cows in the wildebeest's protein budget is therefore clearly evident, since the development of healthy offspring will depend upon the ability of the cows to feed the pre- and post-natal calf.

6.4 SUMMARY

6.4.1

A first approximation of the protein budget of Etosha's wildebeest was attempted by calculating the nitrogen requirements for various life processes. For this purpose, the population was divided into 10 major age-sex and social classes whose numbers and biomass were determined on a seasonal basis.

6.4.2

The nitrogen requirement for maintenance and activity, growth, gestation and lactation was calculated on a seasonal basis by employing suitably modified equations for domestic cattle.

6.4.3

The nitrogen demands were subsequently converted to a protein budget for each class of wildebeest on an individual basis. This enabled a comparison to be made of the mean daily protein requirement between age-sex and social classes for one seasonal year. From this it was evident that reproductive cows had the highest demand for protein throughout the year, namely 199 $g.day^{-1}$ per individual.

6.4.4

The protein budget of the wildebeest population was calculated on a seasonal basis by considering the numerical status of each of the 10 major classes of animal at the midpoint of three seasons. Thereby it was possible to evaluate the seasonal need for protein in each class. Again, the greatest demand was by reproductive cows, which accounted for 51 % of the population's total protein intake.

6.4.5

A yearly population protein budget showed that the estimated 2 493 wildebeest at Etosha required 106 280 kg of protein to meet the demands of free existence. This must be considered a first approximation because of the assumptions made necessary by the absence of nutritional

data for wild African ungulates. It is, however, the first quantified investigation into the protein budget of wildebeest in an unrestrained state.

6.4.6

The findings which have emerged from this study show, with a high measure of confidence, that pregnant and lactating wildebeest cows and their calves are especially vulnerable to a protein deficiency. Together, their protein requirements comprised 65 % of the population's protein budget.

Section 7

NUTRITION : FORAGE YIELDS, FORAGE QUALITY, WATER QUALITY AND ESTIMATES OF FOOD INTAKE AND FAECAL PRODUCTION

7.1 INTRODUCTION

The four basic requirements in a population of wild ungulates, in this case wildebeest, are food, water, protection from climatic extremes, and protection from predators (Sinclair, 1977). Consequently, to identify which environmental factors may limit the wildebeest population at Etosha, it was necessary to quantitatively assess whether sufficient food and water were available and the quality of these two critical factors. Direct monitoring of food intake by oesophageal fistulation of tamed wildebeest has been attempted, but post-surgical complications may develop which require intensive treatment (Usenik *et al.*, 1977) and consequently this method has limitations. Since data on the amount of food ingested by wild ruminants are scarce, indirect methods of estimation may be necessary and have been applied in the case of African buffalo (Sinclair, 1974, 1977) and

Coke's hartebeest (Stanley Price, 1978). Furthermore, the evaluation of forage quality may be undertaken by chemical analysis of faeces (Erasmus *et al.*, 1978). Seasonal food preferences in wildebeest have been noted in several instances (Gwynne and Bell, 1968; Attwell, 1977; Hoppe *et al.*, 1977) and soil factors may play an important role in determining the grassland types and their utilisation by wildebeest (Anderson and Talbot, 1965; Le Roux, 1977).

With these considerations in mind, I attempted a first approximation of the nutritive value of Etosha's grasslands and the quality of available drinking water. For data on the productivity of the grasslands, I referred to the investigation by Le Roux (1977) and to my findings in 1978. An attempt was also made to evaluate the nutritional status of various classes of wildebeest by blood, liver, bone marrow fat and kidney fat analyses (Section 9).

7.2 METHODS

7.2.1 Field Observations

Because culling of wildebeest is not done at Etosha, I

was unable to record any quantified preference for certain grass species. On two occasions a total of 16 wildebeest were shot for veterinary investigation (Section 10) and samples of rumen content were obtained. I was also able to determine, by examining freshly grazed grass tufts in the field, which species were taken by wildebeest. To achieve this it was necessary to watch the grazing animal using a mounted telescope (25x magnification) from a vehicle and then by driving to the point where grazing had been observed. Although this was a rather crude method, with sufficient repetition it did provide a list of grass species commonly eaten by wildebeest. Occasionally fresh carcases of wildebeest provided information on food plants. Furthermore, the spatial and temporal distribution of wildebeest in Etosha was monitored for four consecutive years, at critical seasons, to obtain information on their habitat preferences.

7.2.2 Collection of Grass Samples

In 1976 six areas in Etosha, which comprised the major habitat of the wildebeest population, were sampled for chemical analyses of grass at three stages of growth. Two growth stages, namely sprouting and seeding, were sampled during the wet, hot season (January to April). A third sampling was done at the end of the dry, cold

season (May to August), after the minimum yearly temperatures had occurred and grasses were dormant. In addition, grass from a seventh area, the saline Etosha Pan, was sampled when wildebeest moved onto the Pan. Only two samplings were done in the latter area, one in June when seed was present, and one in August when dormancy was evident. Sprouting grass on the Pan was unavailable to wildebeest because of the inaccessible, wet clay surface. Fig. 7.1 indicates the sampling sites, which were kept constant.

To obtain at least 250 g of oven-dried grass from each area, a minimum of approximately 100 g samples were taken at each of 10 unprotected sites on the plains where wildebeest chose to graze. No attempt was made to collect grass species in proportion to the preference which wildebeest may have for them, since this is unknown at Etosha. However, certain grass species which were grazed by wildebeest were identified (Section 7.2.1), and as they constituted the majority at the sampling sites, it is likely that the samples comprised a high percentage of grass species preferred by wildebeest.

Sampling of each area was carried out as closely to the driest times of day as the distances involved would permit. This was done to ensure minimum amounts of extraneous moisture in the sample. At each sampling point the

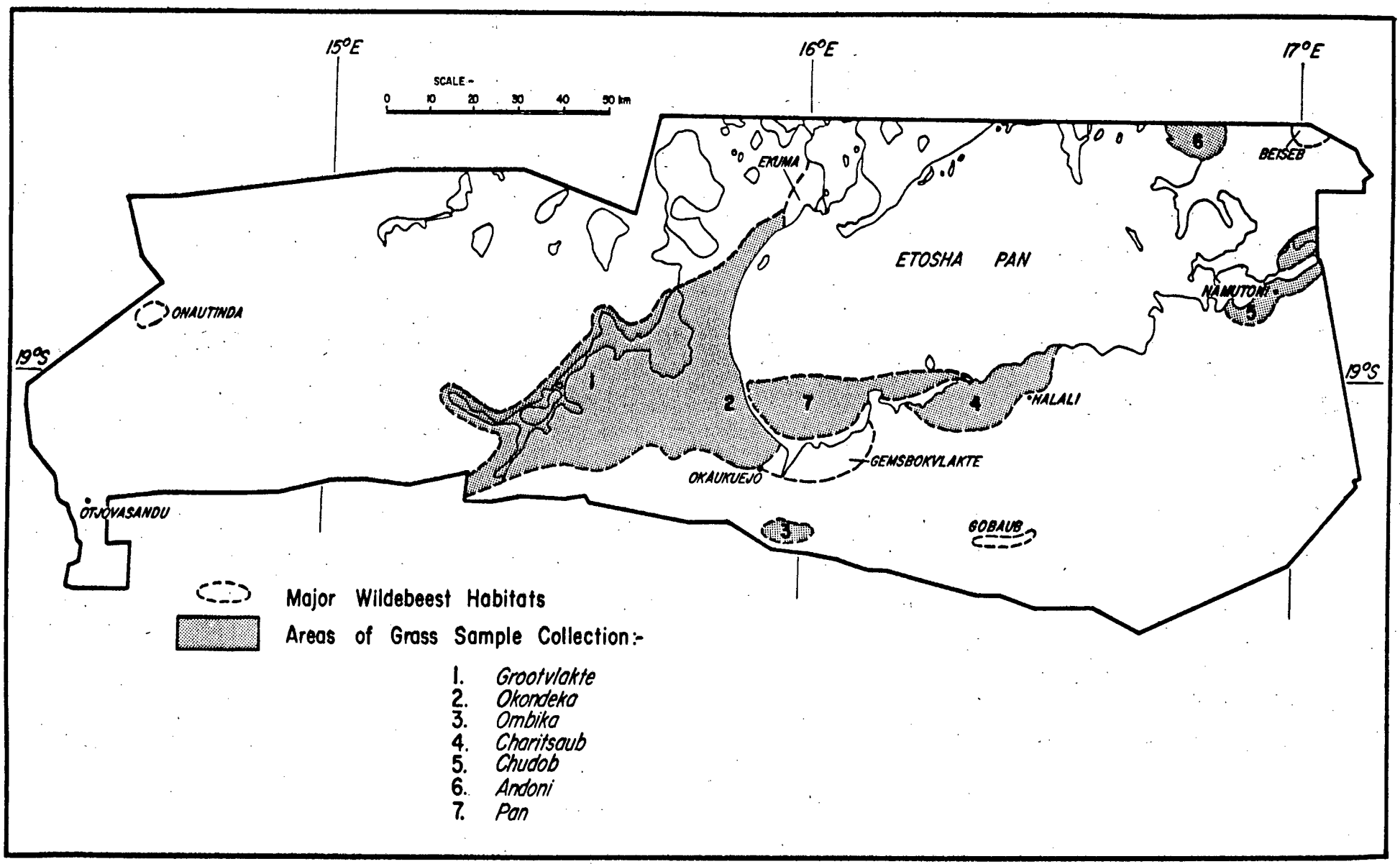

Fig. 7.1 : Major habitats of wildebeest at Etosha from which grass samples were collected for proximate analyses of quality (1976).

dominant grass species were noted before collection. In the sprouting stage, the samples consisted almost exclusively of emerging leaves, whereas at seeding, the inflorescence, stalk and leaves were also collected. During the sampling of dormant grasses, only the leaves and stalks were available. In addition, the prevailing relative humidity and unscreened temperature were recorded at each sampling point.

7.2.3 Determination of Moisture in Grass

Immediately after collection, the samples were placed in sealed air-tight bags and cooled by ice to approximately 0 ^{o}C for transportation to a laboratory. To determine moisture, the mass of each sample in the sealed bag was measured to the nearest 0,01 g. The bag was then opened, the grass transferred to a paper bag and both bags and the grass were placed in a ventilated drying oven at 60 $\pm$ 2 ^{o}C until constant mass was achieved.

7.2.4 Proximate Analyses for Quality of Grass

To reduce costs of analyses, the 10 replicates from each sampling area were combined into three samples by mixing replicates 1 to 3, 4 to 6, 7 to 9, and discarding replicate 10. In this way, adjacent sampling sites were equally

represented in the analyses.

Standard AOAC (1965) methods were used. Crude protein was determined by Kjeldahl and the nitrogen content multiplied by a factor of 6,25 to obtain percentage crude protein. Percentage lipid was determined by ether-hexane extraction. Crude fibre was expressed as a percentage, by boiling in acid and alkali and subsequent ashing. The percentage of nitrogen-free extract was determined by calculating the difference between the summed percentages of crude protein, lipid, crude fibre, ash and 100 %. Energy values were determined by standard bomb calorimetry.

Metabolisable energy was calculated from proximate analyses of the grass samples by application of the formula :

$$M\,E\ (MJ.kg^{-1}) = 0{,}012\ (CP) + 0{,}031\ (EE) + 0{,}005\ (CF) + 0{,}014\ (NFE)$$

Where :

ME = metabolisable energy expressed as Megajoules per kilogram

CP = crude protein ($g.kg^{-1}$)

EE = ether extract ($g.kg^{-1}$)

CF = crude fibre ($g.kg^{-1}$)

NFE = nitrogen-free extract (soluble carbohydrates) ($g.kg^{-1}$)

(Reference : *Energy Allowances and Feeding Systems for Ruminants*. Ministry of Agriculture, Fisheries and Food, Her Majesty's Stationary Office, London, Technical Bulletin 33.)

7.2.5 Faecal Analyses

A total of 45 faecal grab samples were taken from the rectums of immobilised wildebeest, and during post mortems seven samples were collected. In addition, 12 samples of freshly dropped faeces were collected when wildebeest whose age-sex and social class could be determined, were seen defaecating in the veld. To avoid contamination of freshly dropped faeces, only pellets which showed no adhering soil were taken. All faecal samples were immediately placed in air-tight bags and treated similarly to the grass samples (Section 7.2.2 and 7.2.3) for transport and moisture determination. Proximate analyses for crude protein, lipid, crude fibre, ash, nitrogen-free extract and energy values were undertaken as described in Section 7.2.4. In addition, the calcium, phosphorus and magnesium content of six selected faecal samples were determined.

7.2.6 Rumen Contents

The rumen contents of wildebeest were taken from 16

animals shot for veterinary investigation. Eight of these samples were obtained at the height of the wet, hot season, namely March 1978, and eight during the dry, hot season, namely November 1978. The samples were evaluated for structural components only and species were not identified.

Gwynne and Bell (1968) and Attwell (1977) have investigated the rumen contents of free-ranging wildebeest. Their method was followed with modifications, after consideration of the method advocated by Chamrad and Box (1964). The rumen of each animal was opened and the contents transferred to a container where they were manually mixed. Thereafter the contents were spread evenly onto a plastic tarpaulin and five grab samples of 50 ml each were taken at random. These samples were mixed and preserved in standard AFA solution. To quantify structural components of the food of wildebeest, each composite sample was evenly floated with one litre of water in a tray measuring 50 x 50 cm which was gridded into 100 divisions of 5 x 5 cm each. Using an illuminated 10-magnification lens, the food particle nearest to each grid intersection was removed by fine-pointed forceps and placed in a petri-dish. The 100 food particles thus collected were individually examined under an illuminated, binocular dissecting microscope using 6x - 50x magnification. Food particles were classified as grass or non-grass or unidentifiable,

the grass component being further categorised as leaf-blade, leaf-sheath, culm, inflorescence and roots.

In this manner, the percentage occurrence of food components of wildebeest could be obtained on a structural basis. The method's validity has been confirmed by Gwynne and Bell (1968), who found that no significant differences exist between analysis of different sub-samples from the same sample, or between artificial mixtures of known plant components and their analysis by the present method.

7.2.7 Estimation of Productivity

The production of herbage (dry matter) on the grassland plains of Etosha has been estimated by Le Roux (1979), who distinguished between wet season (summer) grazing areas and dry season (winter) grazing areas. I have referred to his findings for the period 1972 - 1977. During the 1977/78 period, herbage production (DM) was determined by myself, following the procedure advocated by Le Roux (1979). In addition to the five major grassland areas measured by Le Roux (1979), I measured productivity of grass on the Etosha Pan and Ombika (Fig. 7.1) during 1977/78. This was considered necessary because wildebeest moved onto the Pan in large numbers during this period but to a much

lesser extent into the Ombika area.

I determined dry matter production by clipping herbage to ground level from 1,0 m^2 frames placed within open-topped wire mesh exclusion plots in the summer grazing areas of Okaukuejo and Namutoni (Fig. 7.1). Because of the area involved at Okaukuejo (102 000 ha), a total of 45 replicates of 1,0 m^2 were harvested from separate exclusion plots erected throughout the area. At Namutoni (6 300 ha), 10 replicates of 1,0 m^2 were harvested at separate exclusion plots. Sampling of these summer grazing areas was done at the end of the growing season (April), when wildebeest began the seasonal migration to winter grazing areas. At the start of migration, a corresponding number of unprotected control plots were harvested from 1,0 m^2 frames placed at random near each exclusion plot to determine the residual yield after grazing. The control plots were in areas which had been grazed by wildebeest and other large herbivores. Consequently, the mass of herbage removed by grazers could be calculated.

No exclusion plots were used in the winter grazing areas. Instead "in-cuts" were made from 1,0 m^2 frames at sites unprotected from grazers when the migrating wildebeest and other large herbivores moved into these areas. A total of 20 replicates of 1,0 m^2 herbage was sampled in the

winter grazing areas of Ombika (1 400 ha), Etosha Pan (20 000 ha), Gemsbokvlakte (13 800 ha), Charitsaub (15 600 ha) and Andoni (4 400 ha). Similarly, 1,0 m^2 "out-cuts" were made from 20 replicates in each of these areas when the herbivores migrated out of these areas to the summer grazing areas in December.

Each sample harvested was divided into three components, where these occurred, namely, grass produced in the season, weeds produced in the season, and accumulated litter from the previous season. Perennial, woody shrubs, which occurred on the grassland, were not harvested, since they did not form part of the wildebeest's diet. After drying in a ventilated oven at 60 $\pm$ 2 ^{o}C until constant mass was achieved, the dry mass of grass, weeds and litter per 1,0 m^2 was measured to the nearest 0,01 g. Grass production was used in the estimate of nutrient quantity available to wildebeest, whereas weeds and litter were indicators of over-utilisation or unused components of the grasslands respectively.

7.2.8 Estimation of Food Intake by Wildebeest

The daily intake of food by free-ranging wildebeest has not yet been determined, although prediction equations for domestic cattle and sheep have been constructed

(Blaxter *et al.*, 1966; Van Soest, 1968; Engels *et al.*, 1978). Also, from the literature it appears that there is no really satisfactory equation for estimating the amount of food ingested by wildebeest and I have accordingly applied a widely accepted "rule of thumb". This states that on green pasture, cattle will consume 3 kg dry matter per 100 kg live body mass and on dry pasture 2 kg dry matter per 100 kg mass (F.J. van der Merwe, pers.comm., 1978). However, the formulae mentioned above were also applied for comparison.

7.2.9 Water Analyses

To evaluate the quality of water which wildebeest drank at Etosha and also to establish whether they showed preference for specific water sources, samples for chemical and microbiological analyses were taken during a period of five years (1974 - 1978). This investigation was undertaken by the National Institute for Water Research (NIWR), Windhoek Regional Laboratory. It formed part of a larger project to survey the quality of water throughout Etosha National Park (Winter *et al.*, 1976, 1977, 1978, 1979). In addition to the comprehensive wet and dry season samplings which were provided by this investigation, I sampled water from perennial fountains and seasonal rainwater pools when wildebeest showed a marked preference to drink from them.

Chemical analyses of these samples were also undertaken by NIWR, Windhoek. Water samples from the Ekuma River were analysed chemically by the Department of Water Affairs (S.W.A. Branch). A total of 69 perennial water sources were sampled and for the purpose of my investigation these were classified as originating from four major sources, namely, man-made boreholes (30), artesian wells (2), natural fountains (36), and river water (1). In addition, I took five samples from seasonal rainwater pools during 1977/78 and these were analysed chemically.

7.2.9.1 Bacteriological Counts

Cultures made from the water samples were inspected for *Escherichia coli*, *Clostridium perfringens*, *Staphylococcus aureus*, enterococcal forms (*Streptococcus faecalis*), and faecal coliform bacteria. In addition, total plate counts were made. Culturing and counts were in accordance with standard bacteriological procedures (Winter *et al.*, 1979).

7.2.9.2 Chemical Analyses

Macro-elements and trace elements in the water samples were determined by standard analytical methods (Winter *et al.*, 1979; Department of Water Affairs, 1977).

7.2.10 Milk Analyses

To determine the composition of wildebeest milk at Etosha, I milked eight lactating cows which had been immobilised and took a milk sample from one cow, shot for veterinary investigation. The samples collectively covered a period of nine months and were individually analysed for fat, protein and lactose (AOAC, 1965). All milk samples were preserved by freezing to -20 $\pm$ 2 ^{o}C prior to analyses.

7.2.11 Kidney Dimensions

The mass of one fresh kidney, taken from each of 16 shot wildebeest (Section 10), was measured to the nearest 0,1 g. Length, width and depth dimensions were determined to the nearest 0,1 mm using a set of calipers. The kidney volume was calculated as the cube root of the product of its dimensions (Sperber, 1944). Thereafter each kidney was bisected medially, allowing measurement of the cortex and medulla widths respectively, at 20 random points along the exposed surface. Means were calculated for each of these sets of measurements and used to estimate the cortico-medullary ratio. The relative thickness of the medulla was obtained by the formula of Sperber (1944) :

$$\frac{\text{Medulla thickness.10}}{\text{kidney size}}$$

7.2.12 Urine Analyses

Fresh urine was drawn off by disposable syringe from the bladders of 14 shot wildebeest (Section 10) and frozen to -20 ± 2 ^{o}C for transport to a laboratory and subsequent analysis. Seven urine samples were taken during the wet season (March) and a further seven samples were taken during the dry season (November). The urine samples were individually analysed to determine the total osmolality, urea, potassium and sodium concentrations. Osmolalities were obtained using an automatic osmometer (Advanced Instruments, Model 6731 RAS). Urea concentration was determined by an enzymatic method (Fawcett and Scott, 1960) and a spectrophotometer set at 546 nm. Concentrations of potassium and sodium were established by flame photometric techniques (Instrumentation Laboratory, IL 243).

7.2.13 Plasma Analyses

Blood was drawn off in a heparinised disposable syringe from the jugular or the heart of seven wildebeest shot in the dry season and seven shot in the wet season (Section 10). Blood samples were also collected from the jugular of 59 wildebeest, immobilised over a period of two years (1976 - 1978). The plasma was drawn off after 15 minutes of centrifuging in a portable clinical centrifuge set at

7 000 rpm and immediately cooled to -20 ± 2 °C using carbon dioxide. The samples were subsequently transferred to a laboratory where they were stored at the same temperature. Analyses were performed by the same methods used for urine (Section 7.2.12).

7.3 RESULTS

7.3.1 Food Plants

Grasses eaten by wildebeest at Etosha are listed in Appendix 12. Their taxonomy is according to Merxmüller (1972) and Volk (1974). Areas of wildebeest habitat which were sampled for proximate analyses of grass (Section 7.2.2) have been included in Appendix 12 and the dominant species in each area are indicated. The only other record of grass species taken by wildebeest at Etosha is by Tinley (1967) and these have been included in Appendix 12. I have occasional records of wildebeest browsing the tips of the woody, halophytic shrub *Salsola tuberculata* during the height of the dry season, namely November - December. This is the only plant other than grass which Etosha wildebeest have been recorded feeding from.

7.3.2 Effects of Season, Growth Stage and Area on Grass Quality

The moisture present in freshly sampled grass at critical stages of growth is given in Appendix 13, together with the prevailing relative humidity and temperature at the sampling sites. The nutritional value of these grass samples is presented as a percentage of dry mass in Table 7.1. Mean moisture in each area's samples, taken from Appendix 13, has been included as a separate percentage of total mass at sampling.

7.3.3 Gross Energy Values of Grass

The gross energy values of grass sampled at Etosha have been expressed in kilojoules per gram and given as a mean for each of the critical stages of growth (Table 7.2).

7.3.4 Metabolisable Energy, Calculated on a Seasonal Basis

Table 7.3 presents the calculated ME which was available to wildebeest and other herbivores during 1976.

7.3.5 Faecal Analyses, on a Seasonal Basis

Dried faecal material was analysed for the same components

Table 7.1 : Proximate analyses of grass samples from the seven major areas inhabited by wildebeest at Etosha (1976). (Percentage moisture was first calculated separately and thereafter the remaining components were determined as a percentage of the total dry mass.)

Growth Stage	Nutrients (% of dry mass)	Area						
		Grootvlakte	Okondeka	Ombika	Charitsaub	Chudop	Andoni	Etosha Pan
Dormant	Crude protein							
	: rep. 1	3,50	4,00	2,60	3,70	5,70	2,80	7,30
	: rep. 2	4,30	2,40	2,80	2,40	5,80	2,40	7,50
	: rep. 3	3,00	2,50	2,90	3,20	6,60	2,50	8,50
	$\bar{x}$	3,60	2,97	2,77	3,10	6,03	2,56	7,76
	Lipid							
	: rep. 1	1,11	1,29	3,21	0,40	8,23	3,70	1,28
	: rep. 2	3,28	1,50	0,49	2,47	7,81	1,65	1,75
	: rep. 3	0,89	1,34	3,33	0,10	7,90	2,25	0,49
	$\bar{x}$	1,76	1,38	2,34	0,99	7,98	2,53	1,17
	Soluble carbo-hydrates (NFE)							
	: rep. 1	59,90	59,80	56,79	59,18	54,38	59,28	60,55
	: rep. 2	56,93	61,19	59,31	58,41	54,70	61,73	59,88
	: rep. 3	60,62	61,25	56,37	59,98	53,81	61,03	60,14
	$\bar{x}$	59,15	60,74	57,49	59,19	54,30	60,68	60,19
	Crude fibre	35,30	34,71	37,24	36,55	31,60	34,15	30,05
	Ash	0,19	0,20	0,16	0,17	0,09	0,07	0,82
	Moisture (n=10)	4,90	5,75	4,11	4,40	8,47	6,40	4,10

Table 7.1 (Continued)

Growth Stage	Nutrients (% of dry mass)	Area						
		Grootvlakte	Okondeka	Ombika	Charitsaub	Chudop	Andoni	Etosha Pan
Sprouting	Crude protein							
	: rep. 1	16,80	17,50	16,70	21,90	20,00	18,10	-
	: rep. 2	17,20	17,60	20,20	22,60	18,30	21,00	-
	: rep. 3	16,90	15,90	18,70	20,80	19,70	17,00	-
	$\bar{x}$	16,97	17,00	18,53	21,76	19,30	18,70	-
	Lipid							
	: rep. 1	3,58	5,61	6,42	5,10	7,90	2,59	-
	: rep. 2	2,04	2,39	2,90	4,78	6,25	1,34	-
	: rep. 3	2,34	5,26	5,33	5,90	7,70	3,25	-
	$\bar{x}$	2,65	4,42	4,88	5,26	7,28	2,39	-
	Soluble carbo-hydrates (NFE)							
	: rep. 1	47,50	52,02	50,51	46,36	47,76	53,47	-
	: rep. 2	48,64	55,14	50,53	45,98	51,11	51,62	-
	: rep. 3	48,64	53,97	49,56	46,66	48,26	53,91	-
	$\bar{x}$	48,26	53,71	50,22	46,34	49,04	53,00	-
	Crude fibre	31,98	24,60	26,29	26,50	24,31	25,78	-
	Ash	0,14	0,27	0,08	0,14	0,03	0,06	-
	Moisture (n=10)	74,39	69,44	71,75	79,47	69,05	77,22	-

Table 7.1 (Continued)

Growth Stage	Nutrients (% of dry mass)	Area						
		Grootvlakte	Okondeka	Ombika	Charitsaub	Chudop	Andoni	Etosha Pan
Seeding	Crude protein							
	: rep. 1	7,40	9,10	6,40	10,70	14,70	8,40	10,40
	: rep. 2	9,70	10,20	8,10	10,10	11,20	8,90	11,30
	: rep. 3	10,30	10,40	9,00	9,90	13,70	8,00	7,70
	$\bar{x}$	9,13	9,90	7,83	10,23	13,20	8,43	9,80
	Lipid							
	: rep. 1	1,03	3,83	3,64	2,55	8,86	3,15	1,44
	: rep. 2	2,54	3,49	2,50	3,40	7,81	3,54	1,99
	: rep. 3	3,00	3,88	2,90	5,50	8,20	1,95	0,90
	$\bar{x}$	2,19	3,73	3,01	3,81	8,29	2,88	1,44
	Soluble carbo-hydrates (NFE)							
	: rep. 1	55,40	51,73	54,66	51,69	44,84	56,18	54,98
	: rep. 2	51,59	50,97	54,10	51,44	49,39	55,29	53,53
	: rep. 3	50,53	50,38	52,80	49,54	46,50	57,78	58,22
	$\bar{x}$	52,51	51,03	53,85	50,90	46,91	56,42	55,58
	Crude fibre	35,27	35,10	35,10	34,90	31,53	32,24	31,88
	Ash	0,90	0,24	0,20	0,16	0,07	0,03	1,30
	Moisture (n=10)	58,15	63,54	63,21	64,26	68,07	57,14	29,44

Table 7.2 : Gross energy values of grass samples from the seven major areas inhabited by wildebeest at Etosha (1976)

Area	Growth Stage	Gross Energy Values ($kJ.g^{-1}$)	
		Mean	S D
Grootvlakte	Dormant	14,80	0,74
	Sprouting	16,91	0,86
	Seeding	16,27	0,65
Okondeka	Dormant	16,35	1,00
	Sprouting	16,18	0,64
	Seeding	16,82	0,53
Ombika	Dormant	16,08	1,90
	Sprouting	16,75	0,33
	Seeding	16,56	0,70
Charitsaub	Dormant	17,07	1,42
	Sprouting	19,02	0,53
	Seeding	16,55	0,57
Chudop	Dormant	15,14	0,11
	Sprouting	17,63	0,87
	Seeding	16,53	0,61
Andoni	Dormant	15,68	1,10
	Sprouting	17,52	1,07
	Seeding	16,39	1,06
Etosha Pan	Dormant	14,92	1,18
	Seeding	15,07	0,48
Mean of all areas	Dormant	15,67	1,20
	Sprouting	17,33	1,12
	Seeding	16,29	0,78

Table 7.3: Metabolisable energy available to wildebeest at Etosha (1976), calculated on a seasonal basis from proximate analyses of grass samples

Area	Growth Stage of Grass	Replicate No.	Metabolisable Energy (Megajoules/kilogram)	Mean ME ($MJ.kg^{-1}$)
Grootvlakte	Dormant	1	10,9150	11,0153
		2	11,2432	
		3	10,8877	
	Sprouting	1	11,3748	11,2139
		2	11,1050	
		3	11,1620	
	Seeding	1	10,7268	10,8893
		2	10,9375	
		3	11,0037	
Okondeka	Dormant	1	10,9874	11,0228
		2	11,0551	
		3	11,0259	
	Sprouting	1	12,3519	12,1596
		2	11,8025	
		3	12,3244	
	Seeding	1	11,2765	11,2440
		2	11,1967	
		3	11,2590	

Table 7.3: (continued)

Area	Growth Stage of Grass	Replicate No.	Metabolisable Energy (Megajoules/kilogram)	Mean ME ($MJ.kg^{-1}$
Ombika	Dormant	1	11,1197	10,9690
		2	10,6533	
		3	11,1341	
	Sprouting	1	12,3801	12,0803
		2	11,7117	
		3	12,1492	
	Seeding	1	11,3038	11,1686
		2	11,0760	
		3	11,1260	
Charitsaub	Dormant	1	10,6821	10,7944
		2	11,0600	
		3	10,6411	
	Sprouting	1	12,0244	12,0543
		2	11,9560	
		3	12,1824	
	Seeding	1	11,0561	11,2808
		2	11,2126	
		3	11,5736	

Table 7.3: (continued)

Area	Growth Stage of Grass	Replicate No.	Metabolisable Energy (Megajoules/kilogram)	Mean ME (MJ.kg^{-1})
Chudop	Dormant	1	12,4285	12,3797
		2	12,3551	
		3	12,3544	
	Sprouting	1	12,7523	12,6608
		2	12,5058	
		3	12,7243	
	Seeding	1	12,3661	12,2992
		2	12,2576	
		3	12,2739	
Andoni	Dormant	1	11,4911	11,2974
		2	11,1506	
		3	11,2506	
	Sprouting	1	11,7511	11,6963
		2	11,4526	
		3	11,8853	
	Seeding	1	11,4631	11,4165
		2	11,5194	
		3	11,2671	
Etosha Pan	Dormant	1	11,2537	11,2262
		2	11,3296	
		3	11,0954	
	Seeding	1	10,9730	10,9856
		2	11,0485	
		3	10,9352	

as the grass samples (Section 7.3.2). The results are expressed as a percentage of dry mass and summarised in Table 7.4, with the detail appearing in Appendix 14. Moisture content of each faecal sample has been included as a separate percentage of the total mass at sampling, when the faeces were fresh. In a few samples, such as those dropped by wildebeest on the Etosha Pan, it was not possible to collect the faeces before a considerable amount of moisture had been lost. Consequently, no moisture determinations were done on these. Results of the faecal analyses for calcium, phosphorus and magnesium are given in Table 7.5.

7.3.6 Rumen Contents

Appendix 15 contains the detailed list of plant parts found in the rumen of wildebeest at Etosha during the wet, hot season (March 1978) and the dry, hot season (November 1978). The mean number of grass components are given in Table 7.6. Seasonal dietary components are collated and presented diagrammatically in Fig. 7.2, together with the mean value for each component.

7.3.7 Grass Yields

Appendices 16 and 17 give the utilisation of grass by large

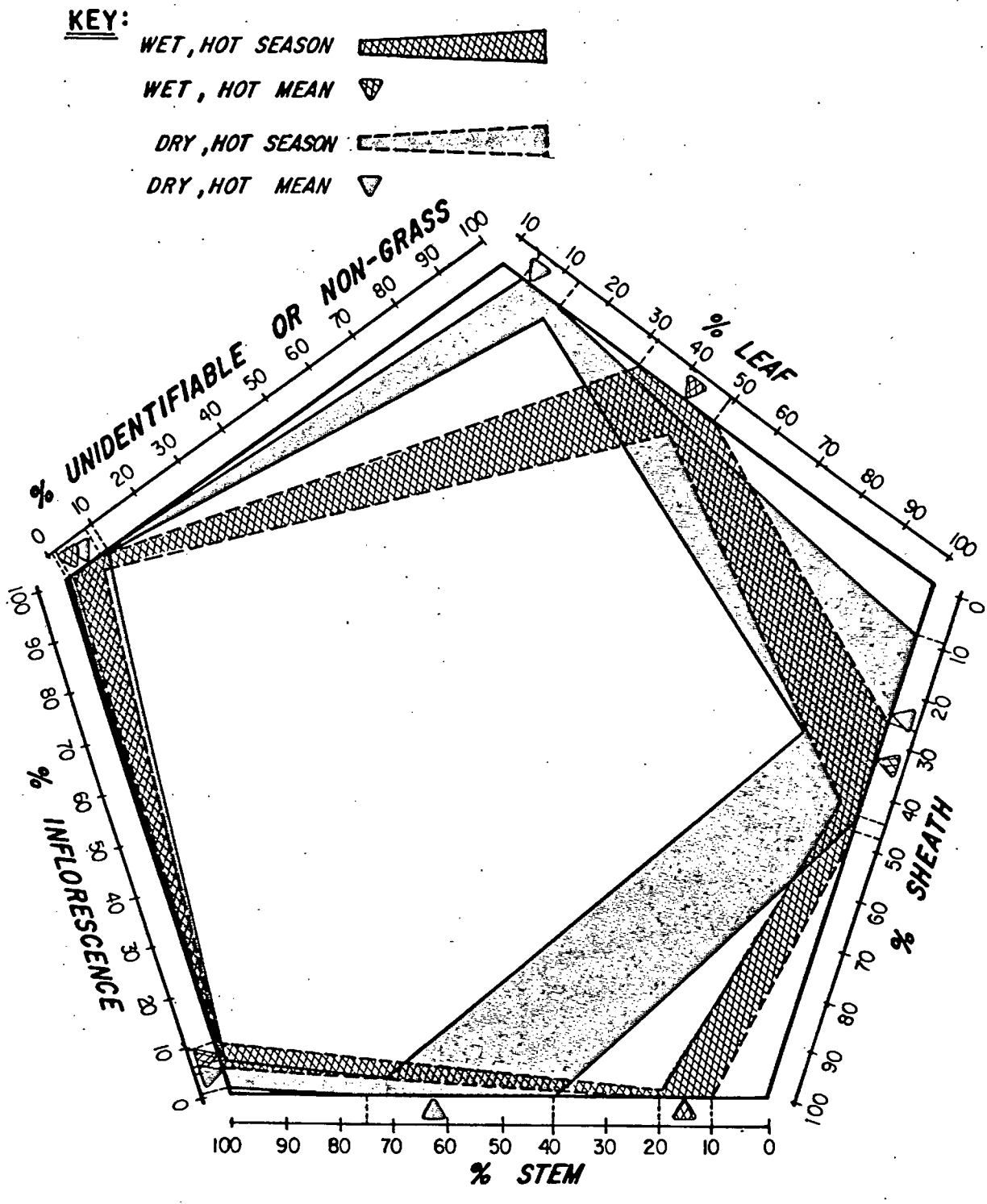

Fig. 7.2 : Frequency of occurrence of five major dietary components in the rumen of wildebeest at Etosha, plotted for the wet and dry seasons of 1978.

Table 7.4 : Mean moisture content and proximate analyses of wildebeest faeces on a seasonal basis at Etosha (1976-1978). The standard deviation is bracketed.

Season	n	Moisture in fresh faeces (%)	Component (% of dry matter)					Gross energy value ($kJ.g^{-1}$)
			Crude protein	Lipid	Soluble carbohydrates (NFE)	Crude fibre	Ash	
Wet, hot (Jan. to April)	24	72,6 (±6,4)	9,0 (±1,4)	2,8 (±0,7)	38,3 (±4,1)	25,3 (±3,6)	26,0 (±3,1)	17,7 (±2,2)
Dry, cold (May to Aug.)	31	68,8 (±3,0)	10,4 (±3,3)	2,4 (±0,3)	46,9 (±3,9)	22,7 (±3,5)	17,6 (±4,3)	18,4 (±2,2)
Dry, hot (Sept. to Dec.)	9	63,7 (±2,9)	7,8 (±0,6)	2,4 (±0,4)	44,1 (±3,9)	20,7 (±1,7)	24,9 (±4,3)	16,4 (±0,8)

Table 7.5 : Proximate analyses of three critical inorganic elements in wildebeest faeces

Season	Age-sex and social class	Inorganic element (%DM)		
		Calcium	Phosphorus	Magnesium
Wet, hot (Jan. to April)	adult, lactating cow	2,55	0,38	1,11
	lone, territorial bull	2,89	0,32	0,70
	adult, bachelor bull	3,89	0,25	1,41
Dry, cold (May to Aug.)	1½ year old bull, mixed herd	2,52	0,23	1,06
	lone, territorial bull	0,90	0,34	0,29
	adult, bachelor bull	2,29	0,28	0,49
$\bar{x} \pm SD =$		$2,51 \pm 0,97$	$0,30 \pm 0,06$	$0,84 \pm 0,42$

Table 7.6: Rumen contents of wildebeest sampled in two critical seasons at Etosha (1978). A total of 100 components were examined per sample. The standard deviation is bracketed.

Season and number of samples	Mean number of grass components					Unidentifiable or non-grass
	Leaf	Sheath	Stem	Inflorescence	Roots	
Wet, hot (March) n = 8	40,9 (±4,4)	34,5 (±5,9)	14,1 (±3,2)	7,3 (±1,4)	0,1 -	3,1 (±1,6)
Dry, hot (November) n = 8	5,5 (±4,4)	24,5 (±10,4)	61,5 (±11,7)	4,0 (±3,3)	0,6 -	3,9 (±2,9)

herbivores on the open plains of Etosha and this is summarised in Tables 7.7 and 7.8. The yield-removal factor has been expressed as a percentage of production. The number of replicates taken by Le Roux (1979) varies due to the loss of exclusion plots through damage by animals.

7.3.8 Calculation of Total Yield of Crude Protein and Metabolisable Energy in Grass

To calculate total yield of crude protein and metabolisable energy, I applied the values obtained for these components at seeding, when the grass was closest to its maximum yield in terms of mass per unit area (Appendices 18 and 19, with summaries in Tables 7.9 and 7.10). Although this cannot be considered as the exact protein and energy yield, it was the most practical estimate possible in the circumstances. The yields of grass in terms of mass at sprouting were not determined. In the case of the Grootvlakte-Okondeka areas, the means for crude protein and metabolisable energy (Tables 7.1 and 7.3) were calculated from the combined replicates for these two areas. This was necessary because Le Roux (1979) treated Grootvlakte and Okondeka as a unit in his assessment of grass yields. The determination of crude protein and subsequent calculation of metabolisable energy was based

Table 7.7: Yields of grass and removal by large herbivores in the wet season grazing areas of Etosha, expressed as metric tons dry mass (1972-78). 1972-77 data from Le Roux (1979); 1978 data from present study.

Area	Seasonal year	Rainfall (mm)	Total yield (tons DM)	Total removal (tons DM)	Percentage utilisation
Grootvlakte - Okondeka (102 000 ha)	1972	412	22 705	3 305	14,6
	1973	217	31 273	8 272	26,5
	1974	560	109 854	17 340	15,8
	1975	346	No	data	collected
	1976	677	120 452	33 354	27,7
	1977	250	17 646	1 632	9,3
	1978	472	70 553	22 675	32,1
Chudop (6 300 ha)	1972	464	2 942	1 740	59,2
	1973	259	2 320	1 578	68,0
	1974	721	8 963	7 518	83,9
	1975	474	No	data	collected
	1976	561	7 855	5 273	67,1
	1977	373	4 050	2 669	65,9
	1978	710	6 081	3 778	62,1

Table 7.8: Yields of grass and removal by large herbivores in the dry season grazing areas of Etosha expressed as metric tons dry mass (1973 - 1978). 1972-77 data from Le Roux (1979); 1978 data from present study.

Area	Seasonal year	Rainfall (mm)	Total yield (tons DM)	Total removal (tons DM)	Percentage utilisation
Charitsaub	1973	274	8 003	4 961	62,0
(15 600 ha)	1974	821	21 991	8 235	37,4
	1975	451	19 941	14 154	71,0
	1976	494	18 236	10 358	56,8
	1977	326	7 084	2 212	31,2
	1978	491	7 192	5 173	71,9
Andoni	1973	259	2 678	766	28,6
(4 400 ha)	1974	721	7 569	638	8,4
	1975	474	8 606	5 073	59,0
	1976	561	12 066	3 888	32,2
	1977	373	7 307	2 236	30,6
	1978	710	8 054	1 751	21,7
Gemsbokvlakte	1973	217	4 678	1 904	40,1
(13 800 ha)	1974	560	12 668	4 733	37,4
	1975	346	No	data	collected
	1976	677	23 024	14 669	63,7
	1977	250	5 368	1 039	19,4
	1978	472	11 744	7 659	65,2

Table 7.8: (continued)

Area	Seasonal year	Rainfall (mm)	Total yield (tons DM)	Total removal (tons DM)	Percentage utilisa-tion
Ombika (1 400 ha)	1978	685	1 553	1 463	94,2
Etosha Pan (20 000 ha)	1978	472	28 830	24 200	83,9

Table 7.9: Maximum and residual yield of crude protein and metabolisable energy in grass produced by the wet season grazing areas at Etosha (1972-78)

Area	Seasonal year	Maximum grass yield (seeding)		Residual grass yield (dormant)	
		Total crude protein (tons DM)	Total ME (tera-joules)	Total crude protein (tons DM)	Total ME (tera-joules)
Grootvlakte - Okondeka (102 000 ha)	1972	2 162	251	636	214
	1973	2 977	346	754	253
	1974	10 458	1 216	3 034	1 019
	1975	No	data	collected	-
	1976	11 467	1 333	2 857	960
	1977	1 680	195	525	176
	1978	6 717	781	1 570	528
Chudop (6 300 ha)	1972	388	36	72	14
	1973	306	29	45	9
	1974	1 183	110	87	18
	1975	No	data	collected	-
	1976	1 037	97	156	32
	1977	535	50	83	17
	1978	803	75	139	29

Table 7.10 : Maximum and residual yield of crude protein and metabolisable energy in grass produced by the dry season grazing areas at Etosha (1973-78)

Area	Seasonal Year	Maximum grass yield (seeding)		Residual grass yield (dormant)	
		Total crude protein (tons DM)	Total ME (terajoules)	Total crude protein (tons DM)	Total ME (terajoules)
Charitsaub (15 600 ha)	1973	819	90	94	33
	1974	2 250	248	426	148
	1975	2 040	225	179	62
	1976	1 866	206	244	85
	1977	725	80	151	53
	1978	736	81	63	22
Andoni (4 400 ha)	1973	226	31	49	22
	1974	638	86	177	78
	1975	725	98	90	40
	1976	1 017	138	209	92
	1977	616	83	130	57
	1978	679	92	161	71
Ombika (1 400 ha)	1978	122	17	3	1
Etosha Pan (20 000 ha)	1978	2 825	317	359	52

on grass sampled for analyses in 1976. My assumption was that at a specified stage of growth, for example seeding, energy and protein did not vary significantly in the same area from year to year (1972 - 1978). Seasonal variation, however, can be expected to occur, as has been demonstrated in Table 7.1 and also by Afolayan and Fafunsho (1978).

7.3.9 Estimation of Food Intake by Wildebeest

Appendix 20 gives my estimation of seasonal food intake by wildebeest at Etosha. The data are summarised in Table 7.11. In applying this, I used the population structure which existed in 1978 (Section 12). In addition, the mean seasonal body mass for each major age-sex and social class was calculated from data presented for population biomass and growth (Section 5.3). Since food intake on a seasonal basis was a prerequisite for determining which parameters of nutrition may be limiting to wildebeest, I used realistic figures for age-sex classes in which body mass changed during the seasons. Thus, in Appendix 20, calves, immatures and sub-adults were allocated an increase in body mass which was based on the mean daily gain in mass for each age-sex class (Section 5.3, Table 5.7). Similarly, seasonal changes in body mass of pregnant cows were applied, using field data from immobilised animals. In the case of non-pregnant

Table 7.11 : Estimation of seasonal food intake by wildebeest at Etosha, based on the population structure during 1978

Age-sex and social class	Total dry matter intake by season (kg)		
	Wet, hot season (Jan. to April)	Dry, cold season (May to Aug.)	Dry, hot season (Sept. to Dec.)
Calves (0-1 yr)	80 546	80 582	86 742
Immature cows (1-2 yrs)	66 971	50 184	53 704
Immature bulls (1-2 yrs)	66 402	48 885	49 483
Sub-adult cows (2-3 yrs)	81 043	54 789	53 582
Sub-adult bulls (2-3 yrs)	72 122	47 867	44 818
Adult, non-pregnant cows	49 410	33 764	30 744
Adult, lactating and pregnant cows	600 494	349 615	370 499
Lone, territorial bulls	146 160	85 608	28 304
Adult bulls in mixed herds	86 760	59 286	58 804
Adult bulls in bachelor herds	291 600	214 635	273 890
Seasonal totals	1 541 508	1 025 215	1 050 570
Yearly total		3 617 293	

cows and bulls, insufficient field data were available to give valid changes in body mass on a seasonal basis and a mean body mass was used for each of these classes during all seasons.

Furthermore, because the population's structure altered from season to season, I allowed an appropriate increase or decrease in certain age-sex and social classes as the seasonal year progressed. These changes were based on my field observations by ground and aerial counts during 1978 (Section 12). For example, I found that calves, immatures and sub-adults underwent a continual decrease in numbers during the seasonal year. In the case of calves a mean loss of 1,16 per day was applied, while for immature cows and bulls the mean daily loss was 0,07 and 0,14 respectively. For sub-adult cows and bulls this loss decreased to 0,05 and 0,10 respectively. For adult wildebeest, the numbers were kept constant during all seasons, although in the case of bulls I made allowance for observed changes in social status during different seasons. In keeping the adult population numerically constant, my assumption was that the mortality which did occur among adults was compensated by a recruitment from sub-adult ranks. As a result of these seasonal changes in the population's number, it can be seen from Appendix 20 that the total population decreased from 2 454 individuals

(midpoint of the wet, hot season) to 2 269 (midpoint of dry, cold season) to 2 083 (midpoint of dry, hot season). This dovetails well with conditions in Etosha, since the synchronised nature of wildebeest calving gave a yearly maximum population in the wet, hot season (2 493 counted by helicopter in March 1978), when the pasture was at its most nutritious. All calculations made in Appendix 20 were based on the midpoint of each season. The length of the seasons was taken as 120 days (January to April), 123 days (May to August) and 122 days (September to December).

7.3.10 Water Analyses

The sampling points for drinking water available to wildebeest are shown in relation to the areas inhabited by wildebeest at Etosha (Fig. 7.3).

7.3.10.1 Occurrence of Bacteria

To simplify the presentation of data, I applied separate means for boreholes, artesian wells and fountains, on a seasonal basis. These means are given in relation to the frequency with which wildebeest were observed to drink from a particular type of water source (Appendix 21). The total bacterial counts are summarised in Table 7.12.

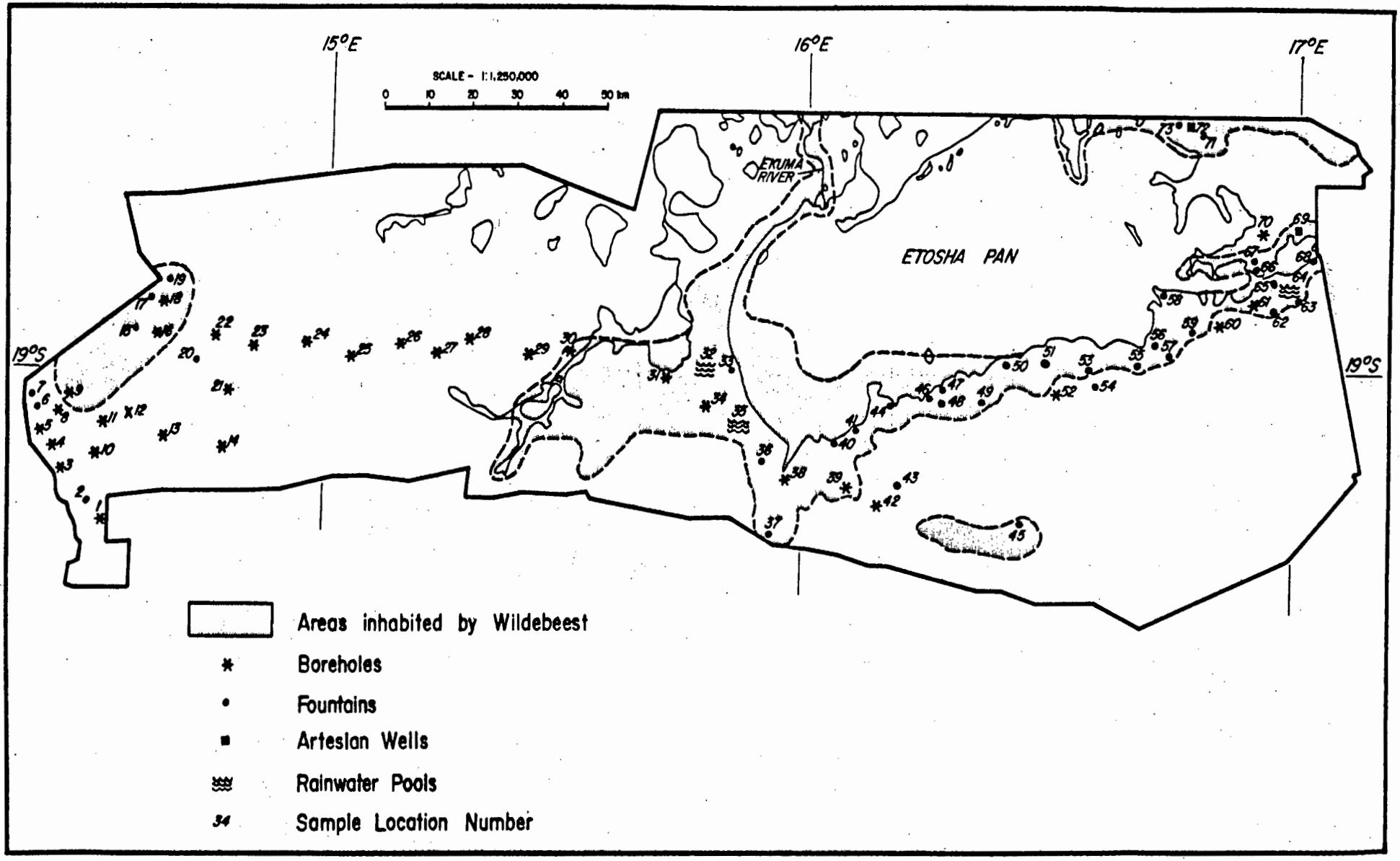

Fig. 7.3 : Sampling points for drinking water available to wildebeest at Etosha (1974-78).

Table 7.12 : Occurrence of bacteria in water sampled from three types of drinking water available to wildebeest at Etosha (1974 - 78)

Origin of water	Year	Season	No. of samples	*Total plate counts/ml	**Relative drinking frequency by wildebeest
Boreholes	1974	Dry	5	2 903	
	1975	Dry	5	1 162	
	1975	Dry	12	23 751	
	1977	Wet	27	11 221	1
	1977	Dry	30	25 549	
	1978	Wet	30	15 382	
	1978	Dry	32	59 806	
Artesian Wells	1974	Dry	2	6 600	
	1975	Dry	2	495	
	1975	Dry	2	735	
	1977	Wet	4	2 225	1
	1977	Dry	4	15 020	
	1978	Wet	1	4 800	
	1978	Dry	3	12 257	
Fountains	1974	Dry	21	7 577	
	1975	Dry	11	2 483	
	1975	Dry	19	8 742	
	1977	Wet	34	4 753	3
	1977	Dry	33	10 388	
	1978	Wet	29	28 306	
	1978	Dry	33	38 962	

*Source : Winter *et al.* (1979); ** 0 = not utilised; 1 = seldom utilised (< 5 % of observations); 2 = infrequently utilised (< 25 % of observations); 3 = commonly utilised (< 50 % of observations); 4 = utilised exclusively when available

To test for seasonal difference in bacterial load at boreholes and fountains, I applied the t statistic for two means to all the values obtained from these two types of drinking water. The results are reflected in Table 7.13. The small number of artesian wells (n = 2) sampled for bacteria did not warrant statistical treatment. In seven out of ten cases, the dry season bacterial counts were significantly higher than the wet season counts (Table 7.13). This was probably due to the concentration of animals at perennial water sources during the dry season. In eight out of ten cases, fountains had significantly higher bacterial counts than boreholes. This may have been because animals waded into the pools created by natural fountains, whereas borehole water was pumped into artificial drinking troughs which were less polluted by faeces and urine.

7.3.10.2 Macro-Elements and Trace Elements

Separate means were calculated for five different types of water on a seasonal basis and are presented in relation to the frequency with which wildebeest drank from them (Appendices 22 and 23). The mean amounts of total dissolved solids (TDS) present and the pH are summarised in Table 7.14.

Table 7.13 : Statistical analysis of seasonal bacterial counts made on boreholes and fountains at Etosha (1974 - 78)

Measurement	Boreholes (Dry vs. wet season)	Fountains (Dry vs. wet season)	Dry season (Fountains vs. boreholes)	Wet season (Fountains vs. boreholes)
Total plate counts (ml^{-1})	+	-	+	+
Total coliforms $(100\ ml)^{-1}$	+	-	-	+
Faecal coliforms $(100\ ml)^{-1}$	+	+	+	+
Clostridia perfringens $(100\ ml)^{-1}$	+	+	+	-
Enterococcal forms $(100\ ml)^{-1}$	-	+	+	+

+ = significantly different ($P < 0,01$)

- = not significantly different ($P > 0,01$)

Table 7.14 : Mean amounts of total dissolved solids and pH in water sampled from five sources available to wildebeest at Etosha (1976 - 78)

Origin of water	Season	* Mean TDS	* pH	** Relative drinking frequency by wildebeest
Boreholes	Dry	1 615	7,9	1
(n = 33-36)	Wet	1 778	7,8	
Artesian wells	Dry	15 233	9,0	1
(n = 2)				
Fountains	Dry	3 055	8,1	3
(n = 28-33)	Wet	2 380	7,9	
Ekuma River	Dry***	39 493	9,6	1
(n = 4)	Wet	17 846	10,0	
Rainwater pools	Wet	504	8,2	4
(n = 5)				

Sources : * Winter *et al.* (1979)
** Refer Table 7.12
*** Dept. of Water Affairs, S.W.A. Branch (Lab. Nos. C 15152-4; 1977)

Seasonal differences in occurrence of macro-elements and trace elements at boreholes and fountains were tested, applying the t statistic for two means to all values obtained from these two types of drinking water (Table 7.15). No statistical analysis was done on results obtained from artesian wells, river water or rainwater, because of the small number of samples. Furthermore, elements which reflected zero values in the dry or wet seasons, such as nitrite, ammonia and phosphate, were not tested statistically. In the case of boreholes, the levels of fluoride and iodine were significantly greater during the dry season, whilst bromide was significantly higher during the wet season. Fountains had significantly more nitrates and fluoride and a higher alkalinity during the dry season, whilst potassium was significantly higher during the wet season. Although only seven out of 32 chemical measurements were significantly different (Table 7.15), it appeared that the water quality of both boreholes and fountains improved generally during the wet season, deteriorating in the dry season. This pattern fitted the predictable influence of rainfall on water quality.

7.3.11 Milk Analyses

The composition and gross energy value of wildebeest milk

Table 7.15 : Statistical analysis of the seasonal levels of macro-elements and trace elements in boreholes and fountains at Etosha (1978)

Measurement	Dry season vs. wet season	
	Boreholes	Fountains
TDS	-	-
SO_4	-	-
NO_3-N	-	+
F	+	+
Na	-	-
K	-	+
Ca	-	-
Mg	-	-
Cl	-	-
SiO_2	-	-
Total alkalinity	-	+
Conductivity	-	-
Trace elements :		
Sr	-	-
Br	+	-
I	+	-
B	-	-

\+ = significantly different ($P < 0,05$)

\- = not significantly different ($P > 0,05$)

is given in Table 7.16. The results show that wildebeest milk had approximately the same amount of lactose as milk from a domestic cow (Maynard and Loosli, 1962), but was much richer in fat and protein.

7.3.12 Renal Function

7.3.12.1 Kidney Efficiency

The kidney dimensions established for wildebeest are given in Table 7.17 and compared with dimensions of other mammalian kidneys (Table 7.18). From this comparison it can be seen that wildebeest have a mean relative medullary thickness of 4,8 which is lower than springbok and bontebok and equals that of the domestic cat.

7.3.12.2 Plasma and Urine Analyses

The results of the plasma and urine analyses of wildebeest are given in Tables 7.19 and 7.20 respectively. A comparison of the maximum plasma : urine osmotic ratio for wildebeest with that found in other mammals has been made in Table 7.18. Wildebeest plasma was found to have typical bovine characteristics (Belonje, 1978) and the plasma : urine osmotic ratio corresponded well with the relative medullary thickness.

Table 7.16 : Composition and gross energy value of wildebeest milk at Etosha (1977-78)

Estimated age of cow (yrs)	Calf present/absent	Composition (% W/W)		
		Fat	Protein	Lactose
8 - 10	Present	13,41	6,88	4,79
5 - 6	Present	7,01	5,77	5,16
4 - 5	Present	9,34	5,60	4,65
5 - 6	Present	12,96	6,22	4,84
3 - 4	Present	15,10	5,56	4,35
6 - 7	Absent	15,10	5,45	4,09
3 - 4	Present	8,10	5,40	5,04
4 - 5	Present	8,24	5,68	5,19
10 - 12	Present	6,67	4,51	5,31
Mean		10,66	5,67	4,82
± SD		±3,46	±0,64	±0,41
Gross energy value in fluid milk :				
(kcal/100 g)		97,22	30,62	18,80
($J.g^{-1}$)		4,068	1,281	0,787

Table 7.17 : Kidney dimensions of wildebeest at Etosha (1978)

Measurement	No. of replicates	Mean	±SD	Range
Mass (g)	16	193,2	±67,3	70,9 - 370,1
Size (mm^3)	16	63,4	± 7,4	46,3 - 72,0
Cortex (%)	320	39,2	± 2,3	34,5 - 44,6
Medulla (%)	320	60,8	± 2,3	55,5 - 65,5
Cortico-medullary ratio	320	1:1,55	± 0,2	1:24 - 1:1,90
Relative medullary thickness	320	4,8	± 0,2	4,5 - 5,3

Table 7.18 : Comparison of relative medullary thickness and maximum plasma : urine osmotic ratios of wildebeest and other mammals

Species	*Relative medullary thickness	Maximum plasma : urine osmotic ratio
Beaver[1] *Aplodontia rufa*	1,3	1 : 2,7
Man[2] *Homo sapiens*	3,0	1 : 4,2
Cat[1] *Felis domesticus*	4,8	-
Bontebok[3] *Damaliscus dorcas dorcas*	4,9	1 : 5,4
Wildebeest[4] *Connochaetes taurinus*	4,8	1 : 5,7
Springbok[5] *Antidorcas marsupialis*	5,5	1 : 8,3
Ground squirrel[6] *Xerus inauris*	12,4	1 : 14,9**
Desert mouse[1] *Psammomys obesus*	12,9	1 : 17,0

*Calculated as : $\frac{\text{medulla thickness (mm)} \cdot 10}{\text{kidney size}}$

**Theoretical maximum

Sources : Chew (1965)[1]
Gordon (1972)[2]
Van Zyl (1979)[3]
Present study[4]
Hofmeyr and Louw (1979)[5]
Marsh *et al.* (1979)[6]

Table 7.19 : Plasma analyses of wildebeest at Etosha (1976 - 78)

Measurement	No. of replicates	Mean	±SD	Range
Osmolality (mOsm/kg)	7	260	±9,0	248 - 276
Urea (mmol/l)	66	6,6	±0,95	3 - 6
Potassium (mmol/l)	7	5,6	±0,98	4 - 7
Sodium (mmol/l)	7	138	±8,0	125 - 149

Table 7.20 : Urine analyses of wildebeest during wet and dry seasons at Etosha (1978)

Measurement	Season	No. of replicates	Mean	±SD	Range
Osmolality (mOsm/kg)	Wet	12	1 008	± 153,0	804 - 1 192
	Dry	7	1 126	± 261,0	720 - 1 520
Urea (mmol/l)	Wet	12	239,7	± 69,9	130 - 337
	Dry	7	257,0	± 69,7	131 - 331
Potassium (mmol/l)	Wet	12	430,9	± 140,0	223 - 739
	Dry	7	142,1	± 169,5	55 - 525
Sodium (mmol/l)	Wet	12	16,2	± 25,3	1 - 71
	Dry	7	583,9	± 222,0	286 - 941

When the seasonal differences in wildebeest urine were examined, applying the t statistic for two means, it was found that osmolality and urea did not vary significantly between the wet and the dry seasons ($P > 0,1$). However, potassium levels of the urine were significantly greater in the wet season ($P < 0,01$), having increased by a factor of 3,0. The mean seasonal sodium levels in the urine were inversely related to those established for potassium, namely a significantly higher level of sodium in the dry season than in the wet season ($P < 0,01$). The factor of increase in sodium was 36,0.

7.4 DISCUSSION

7.4.1 Comparison of Methods for Estimating Food Intake

The results of four methods which I will now discuss are given quantitatively in Table 7.21. To validate the estimate of food intake by wildebeest which has been used in this thesis (Table 7.11), I also applied and compared the equations for domestic stock which have been suggested by other workers.

Table 7.21 : Comparison of methods used to estimate food intake by wildebeest at Etosha

Method	DM intake (tons)			
	Wet, hot season	Dry, cold season	Dry, hot season	Yearly total
Blaxter *et al.* (1966)	1 823	1 808	1 817	5 448
Van Soest (1968)	1 069	917	810	2 796
Engels *et al.* (1978)	1 618	1 620	1 334	4 572
Present study (Table 7.11)	1 547	1 025	1 051	3 617
Means	1 514	1 343	1 253	4 108

7.4.1.1 The Equation of Blaxter *et al.* (1966)

This states that

$$g\ DM.\ kg\ W^{0,73} = 2,33\ DE - 54,2$$

where g DM = grams dry matter intake per day

kg W = live mass in kilograms

DE = digestibility of the food's energy

Furthermore, DE can be calculated if GE and ME are known (Tables 7.2 and 7.3), since energy loss in urine and methane of digestion are reasonably constant at 18 % of DE (Reid, 1968).

Thus $$DE = \frac{ME \times 100}{(100-18)} / GE$$

For example, the equation of Blaxter *et al.* (1966) applied to wildebeest calves with a mean mass of 33 kg (Appendix 20, wet, hot season) was

$$g\ DM.\ 33^{0,73} = (2,33 \times 85,6) - 54,2$$

$$= 145,25\ g \times 12,84\ kg$$

$$= 1,87\ kg\ DM\ per\ 33\ kg\ calf\ per\ day$$

In this equation the digestibility of the energy was calculated as :

$$DE = \frac{11,7445 \times 100}{82} / 16,7233$$

$$= 85,6\ \%$$

where ME = mean metabolisable energy of sprouting and seeding grass during the wet, hot season (Table 7.3)

GE = mean gross energy of this grass (Table 7.2).

In determining these means, I used data from those areas at Etosha where wildebeest grazed during the wet, hot season, namely Grootvlakte, Okondeka and Chudop.

In a similar manner, the daily food intake for each remaining age-sex and social class of wildebeest was calculated using relevant data from Appendix 20.

To calculate DM intake during the dry, cold and dry, hot seasons, a digestibility of 84,7 % of the gross energy was used. This was obtained from the mean ME and the mean GE of dormant grass eaten during these seasons. Areas where wildebeest grazed during the dry seasons were Ombika, Charitsaub, Andoni and Etosha Pan and therefore their data were used (Tables 7.2 and 7.3). Seasonal and yearly

estimates of food intake by the equation of Blaxter *et al.* (1966) are given in Table 7.21.

7.4.1.2 The Equation of Van Soest (1968)

The equation proposed is for voluntary, DM intake by sheep. In addition, I have taken the metabolisable energy into account. The modified equation is :

$$(gDM.W_{kg}^{O,75}) \times (ME_f)$$

where ME_f = factor for metabolisable energy.

Because Van Soest (1968) lists various forages, I chose those which would be the most comparable to Etosha's grasses. Consequently, the forage most representative of the wet, hot season at Etosha was early and mature orchard grass (voluntary intake by sheep is 78 g and 29 g per $W_{kg}^{O,75}$ respectively). I applied a mean value of 54 $g.W_{kg}^{O,75}$. Similarly, mature orchard grass and good brome grass (29 g and 63 g per $W_{kg}^{O,75}$ respectively) were used to represent the dry, cold season at Etosha ($\bar{x}$ = 46 $g.W_{kg}^{O,75}$). For the dry, hot season at Etosha, I chose values given for mature orchard grass and mature brome grass (29 g and 51 g per $W_{kg}^{O,75}$ respectively; $\bar{x}$ = 40 $g.W_{kg}^{O,75}$).

Applying these mean values of voluntary daily food intake to each age-sex and social class of wildebeest (Appendix 20), and taking into account the metabolisable energy at Etosha, the total daily food intake was estimated.

For example, the DM intake of wildebeest calves with a mean body mass of 33 kg (Appendix 20; wet, hot season) was estimated as :

$$(54 \text{ g.} 33^{0,75}_{kg}) \times (\frac{100}{70,2} = 1,42)$$

$$= 1,06 \text{ kg DM per 33 kg calf per day.}$$

Similarly, calculations were made for each age-sex and social class of wildebeest on a seasonal basis, using relevant data from Appendix 20. The estimates obtained are shown in Table 7.21.

7.4.1.3 The Equation of Engels *et al.* (1978)

This equation is based on the voluntary intake of dry, organic matter by lactating and dry Afrikaner cows over a period of five months (November 1971 to March 1972).

For lactating cows, the mean daily intake was found to be $149,38 \text{ g.} W^{0,75}_{kg}$ and the mean daily intake of dry cows was $98,38 \text{ g.} W^{0,75}_{kg}$.

Because these equations consider only the intake of organic matter, I added the mean mass of ash present in Etosha's grasses, namely 0,2 g per 100 g grass (Table 7.1), to obtain an improved estimate of total daily intake by wildebeest. Thus I assumed that lactating wildebeest would ingest 149,68 $g.W_{kg}^{0,75}.day^{-1}$ and all other wildebeest would ingest 98,68 $g.W_{kg}^{0,75}.day^{-1}$. Calculations were then made for each age-sex and social class on a seasonal basis, using relevant data from Appendix 20. The estimates obtained are shown in Table 7.21.

7.4.1.4 Method Used in the Present Study

The well-known "rule of thumb" used by agriculturalists for domestic cattle forms the basis of estimating food intake by wildebeest in the present study (Section 7.3.8 and Table 7.11). Thus, during the wet, hot season, the food intake was estimated to be 30 g $DM.kg.day^{-1}$ and during the dry, cold and dry, hot seasons it was 20 g $DM.kg.day^{-1}$.

Comparing the results obtained by this and other methods (Table 7.21), it can be seen that the method I have employed produces data which are within the range given by three other prediction equations. These other methods give a yearly DM intake of 2,8 kiloton (Van Soest, 1968),

5,4 kiloton (Blaxter *et al.*, 1966) and 4,6 kiloton (Engels *et al.*, 1978). The method I have chosen gives a yearly DM intake of 3,6 kiloton and falls within the lower range of the four estimates ($\bar{x}$ = 4,1 kiloton).

7.4.2 Comparison with Grass Quality in Other Areas

I wished to compare the nutritive value of the study area's grasses with that of other grasslands. Table 7.22 makes this comparison, using as references three areas in which wildebeest currently occur or have been recorded. It is evident that grass from the wildebeest habitat at Etosha contained, on average, more than twice the percentage of crude protein during the wet season than other areas inhabited by wildebeest in Africa. In spite of this, one of these, the Serengeti Plains, supported a population of 1,4 million wildebeest during 1978 (Sinclair, 1978, pers. comm.), which is the largest in existence. The Athi Plains of Kenya also supported up to 9 000 wildebeest (Talbot and Talbot, 1963), whilst the Central Transvaal grassveld was previously inhabited by large numbers of wildebeest (Sidney, 1965).

The level of crude protein available to wildebeest at the midpoint of the dry season (August) in Etosha remained higher than that found in other areas. However, it is

Table 7.22 : Crude protein and gross energy from grass available to wildebeest in three of four areas in Africa. The Central Transvaal grassveld was previously inhabited by wildebeest (Sidney, 1965).

Area	Source of data	Season	Crude protein (%)		Energy ($kJ.g^{-1}$)	
			Range	Mean	Range	Mean
Athi Plains	Stanley Price	Wet	4,53 - 5,13	4,83	17,03 - 17,23	17,13
(Kenya)	(1978)	Dry	2,90 - 4,33	3,62	16,67 - 16,93	16,80
Serengeti Plains	Sinclair	Wet	5,06 - 9,87	6,58	-	-
(Tanzania)	(1974)	Dry	2,18 - 5,22	3,60	-	-
Central Transvaal grassland	Joubert	Wet	4,30 - 7,20	5,70	-	-
(South Africa)	(1954)	Dry	3,40 - 4,70	3,78	-	-
Etosha National Park	Present Study	Wet	7,83 - 21,76	13,91	15,75 - 17,81	16,78
(South West Africa)		Dry	2,56 - 7,76	4,11	14,90 - 18,70	15,72

likely that there would be a continued decrease in crude protein as the dry season reached its zenith during December. This premise is based on the fact that cumulative grazing pressure during the dormant period (September - December) resulted in depletion of grass leaf and a concomitant increase in fibrous components, such as stem (Table 7.6). Concentrations of crude protein are highest in the leaf, lower in the sheath, and least in the stem (Sinclair, 1974; Stanley Price, 1978).

Gross energy (GE) values for wet and dry seasons are available from the Athi Plains (Stanley Price, 1978) and are very similar to the levels encountered seasonally in Etosha's grasses. However, the percentage of ME in relation to GE is considerably lower in grass from ruminants' stomachs collected on the Athi Plains than that calculated for Etosha. For instance, the actual ME intake in Coke's hartebeest was 40,7 % of the GE intake (Stanley Price, 1978) while analyses of Etosha's grasses available to wildebeest gave a calculated ME/GE relationship of 69,9 %.

7.4.3 Minimum Crude Protein Requirements and Effect of Food Selection in Wildebeest

Protein is probably the most important nutritive component

in the diet of ruminants, such as African buffalo and wildebeest (Sinclair, 1974). Furthermore, there is a minimum level of crude protein required to maintain nitrogen equilibrium in a healthy animal. Below this the animal enters "negative nitrogen balance" which results in a deficiency of amino acids and the animal's "condition" deteriorates (Maynard and Loosli, 1962). This minimum level of crude protein has been estimated to be between 4 - 8 % for domestic cattle in the tropics (Agricultural Research Council, 1965). A minimum level of 5 % was applied in the case of free-ranging African buffalo (Sinclair, 1974) and I propose to use it as a critical nutritive level for wildebeest. Accordingly, the seasonal changes in percentage crude protein available to wildebeest at Etosha have been illustrated in Figs. 7.4 and 7.5. It must be noted that the crude protein levels presented only indicate the availability of this critical nutrient. The very significant effect of selection of grass components by grazing wildebeest (Gwynne and Bell, 1968; Attwell, 1977; Table 7.6 of this study) must also be considered. The absence of upper incisors in a wildebeest's mouth and the substitutive hard pad of tissue against which the lower incisors close, serves to act as a trapping mechanism which pulls material from the plant (Gwynne and Bell, 1968). Thereby, grass components such as leaf and sheath, which are rich in

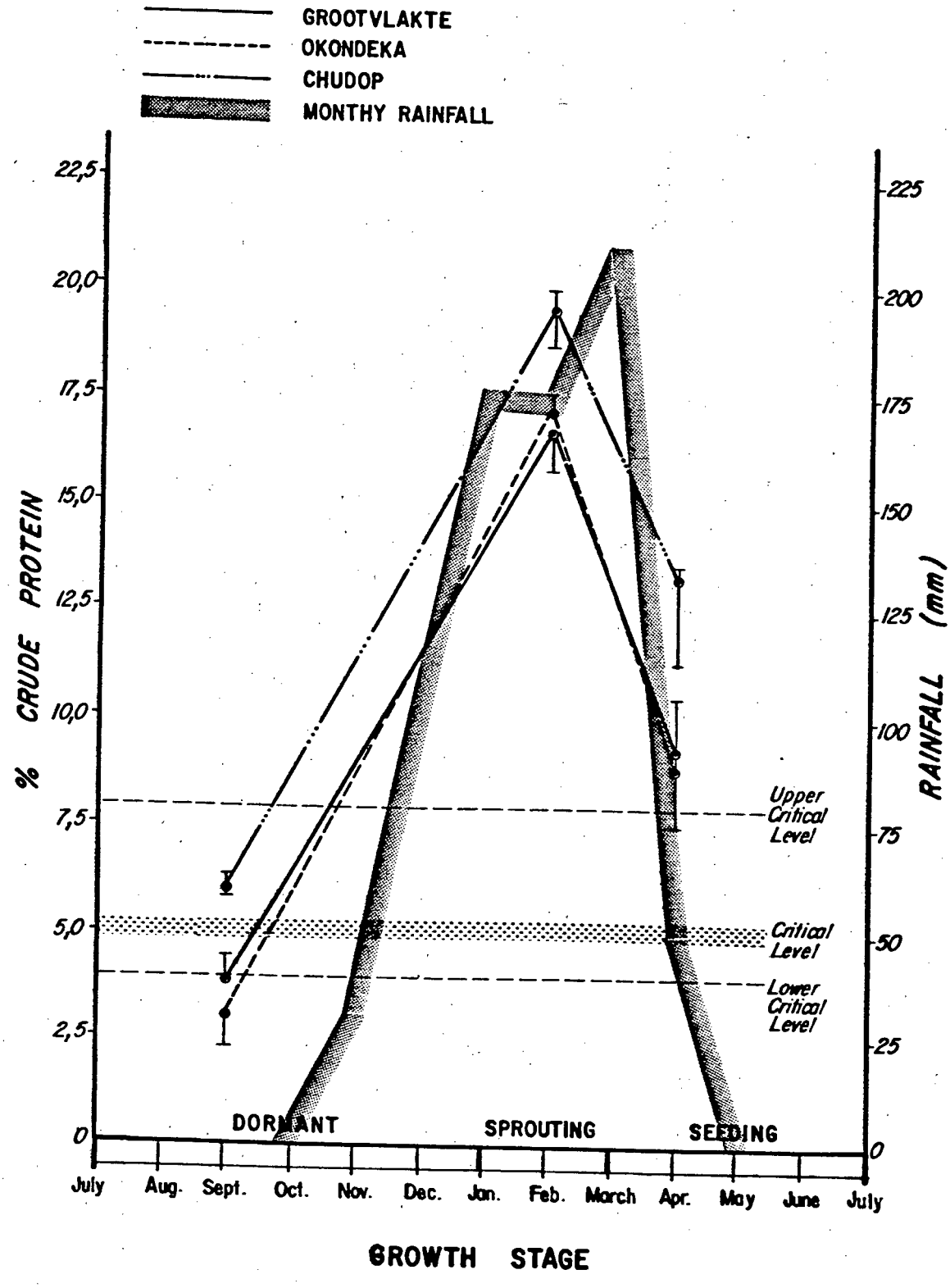

Fig. 7.4 : Seasonal changes in mean percentage crude protein of grass from wet season grazing areas preferred by wildebeest at Etosha (1976).

T-bars show range of values.

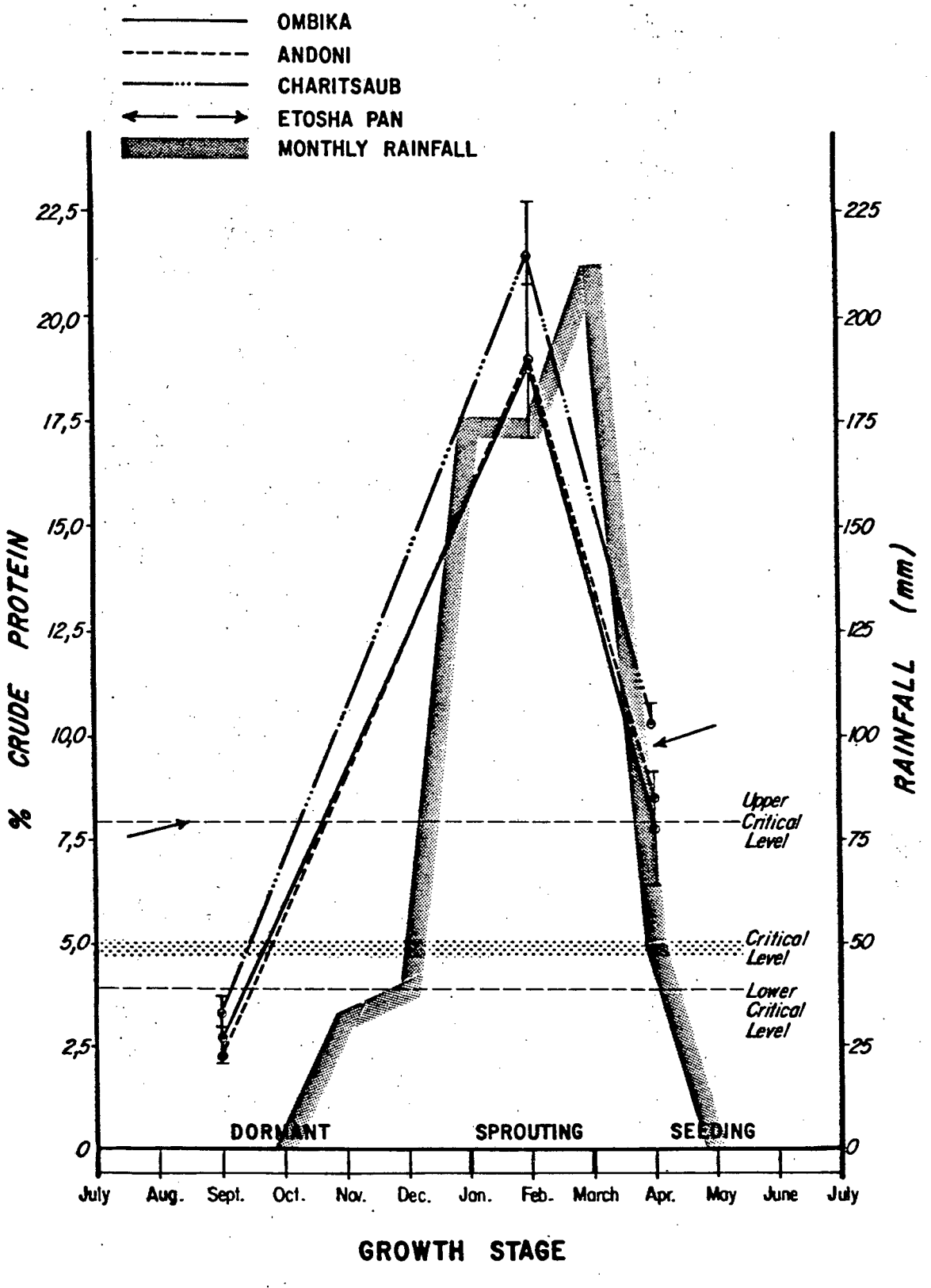

Fig. 7.5 : Seasonal changes in mean percentage crude protein of grass from dry season grazing areas preferred by wildebeest at Etosha (1976).

T-bars show range of values.

protein, are selectively stripped from the more fibrous stem by grazing wildebeest. At certain seasons the structural composition of the pasture facilitates the selective ability inherent in the morphology of wildebeest mouths. This phenomenon is clearly evident at Etosha where there is an abundance of leaf and inflorescence in grasses during the wet season and a decline of these components as the dry season approaches its zenith. Obviously then, the protein-rich leaf will be more readily available to wildebeest during the wet season, but although the fibrous stem with its low nutritive value predominates in the dry season, the selective feeding of wildebeest will partially compensate for this.

A comparison of the selective grazing exhibited by wildebeest in various areas of Africa has been made in Table 7.23. From the data presented it was evident that wildebeest ingested more grass leaf than any other plant component during the wet season. Seasonal intake of grass sheath varied considerably between areas and this may have been related to the relative availability of sheath. It may also have been related to the structural qualities of the different grass species found in these areas which could affect the ability of wildebeest to strip sheath from stem. However, if the intake frequency of stem during the wet season is

Table 7.23 : Mean seasonal frequency of food components in the rumen of wildebeest from different areas of Africa

Area	Season	Food component						Percentage grass in rumen
		Grass					Non-grass or unidentifiable	
		Leaf	Sheath	Stem	Inflorescence	Roots		
Serengeti National Park Tanzania[1]	Wet	61,33	28,92	8,00	-	-	1,75	98,67
	Dry	17,20	52,70	30,10	-	-	-	100,00
	Combined	39,27	40,81	19,05	-	-	0,87	99,34
Serengeti National Park Tanzania[2]	Combined	17,00	-	30,00	-	-	-	98,00
Umfolosi Game Reserve Zululand[3]	Wet	53,00	13,70	29,30	-	-	4,00	96,00
	Dry	35,50	13,60	46,90	-	-	4,00	96,00
	Combined	44,25	13,65	38,10	-	-	4,00	96,00
Etosha National Park South West Africa[4]	Wet	40,90	34,50	14,10	7,3	0,1	3,10	96,90
	Dry	5,50	24,50	61,50	4,0	0,6	3,90	96,10
	Combined	23,20	29,50	37,80	5,7	0,3	3,50	96,50

Sources : Gwynne and Bell (1968)[1]
Sinclair (1974)[2]
Attwell (1977)[3]
Present study[4]

compared between areas, it can be seen that the situation on the Etosha grasslands is similar to that on the Serengeti Plains, namely a low percentage of stem in the diet. At Serengeti 99 % of the plains' vegetation is grass (Sinclair, 1974) and at Etosha, areas such as Andoni and the Etosha Pan support pure stands of grass. An additional common factor is that wildebeest prefer the shorter grass (3 - 40 cm, Sinclair, 1974; and < 50 cm, pers.obs.). If the situation at Umfolosi Game Reserve is examined (Attwell, 1977) the relatively high intake of stem during the wet season by wildebeest indicates that they were utilising taller grass stands. Furthermore, it underlines the nutritive advantage to wildebeest on short grass with a high crude protein content. The woodland-tall grassland habitat prevailing at Umfolosi (Attwell, 1977) will, by comparison, produce lower levels of crude protein for wildebeest.

7.4.4 Nutrient Differences in Growth Stage of Grass for the Preferred Grazing Areas

The seasonal variation in levels of crude protein (Section 7.4.3) are related to corresponding changes in other nutrients and indigestible components of the grass (Figs. 7.6 and 7.7). Fluctuations in nutrients may cause a preference in wildebeest for particular areas

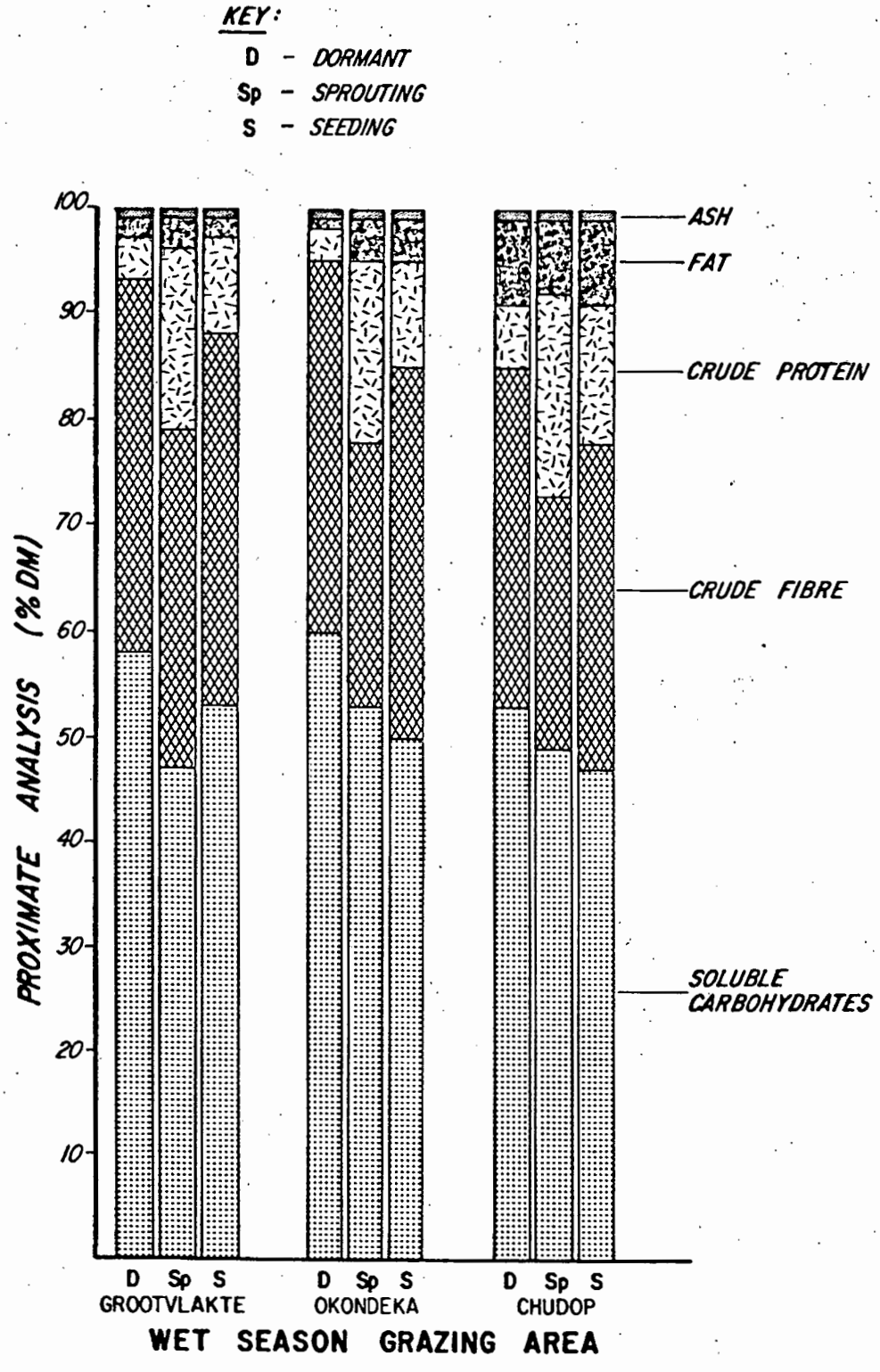

Fig. 7.6 : Seasonal changes in grass quality from three major areas inhabited by wildebeest at Etosha during the wet season (1976).

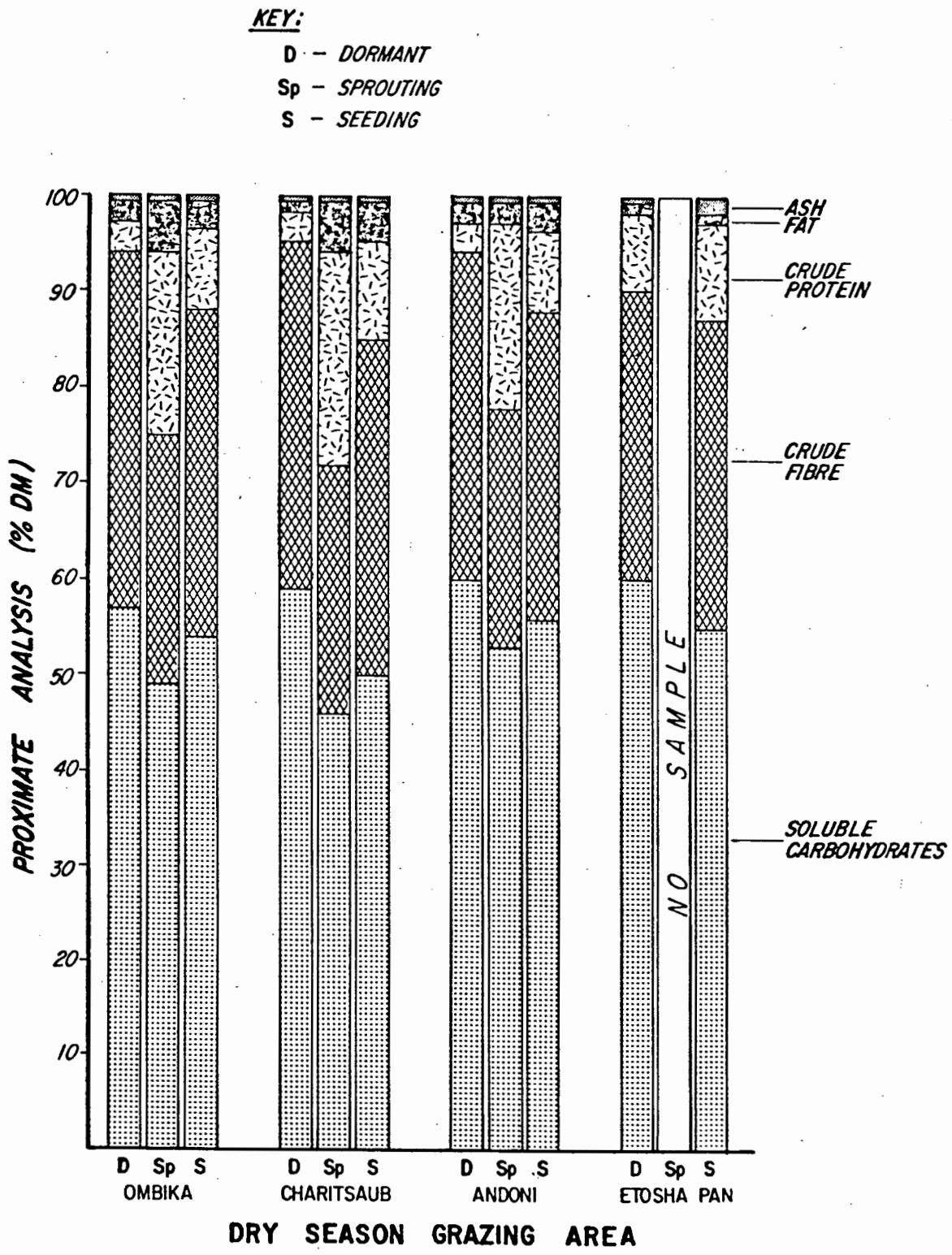

Fig. 7.7 : Seasonal changes in grass quality from three major areas inhabited by wildebeest at Etosha during the dry season (1976).

(Anderson and Talbot, 1965). Consequently, I examined the nutrient levels of grass at critical growth stages and made comparisons between these levels and the different areas at Etosha which wildebeest preferred to graze.

7.4.4.1 Soluble Carbohydrates

Soluble starches and sugars make up the nitrogen-free extract (NFE) component of carbohydrates. These are easily digested, being converted to a source of high energy (Moen, 1973). NFE comprised the greatest percentage DM of Etosha's grass from all areas sampled and in all seasons (46,3 - 60,7 %). They were lowest at the sprouting stage ($\bar{x}$ = 50,1 % $\pm$ 2,8 %) increasing during seeding ($\bar{x}$ = 52,5 % $\pm$ 3,2 %) and reached their highest level at dormancy ($\bar{x}$ = 58,8 % $\pm$ 2,3 %).

To test for seasonal and area differences in NFE, I applied the t statistic for two means, which is permissible, since this test is sufficiently robust to allow the use of percentages (Sokal and Rohlf, 1969). NFE levels at seeding were significantly higher than at sprouting ($P < 0,05$), whilst dormant levels were much greater than seeding levels ($P < 0,01$). However, although wet and dry season grazing areas did not differ significantly in NFE

at the sprouting and dormant stages of growth ($P > 0,05$), dry season grazing areas had higher levels of NFE at seeding ($P < 0,01$). Consequently, there was an increasing percentage of highly digestible energy available to wildebeest from sprouting of grass to its dormant stage in both the wet season and the dry season grazing areas of Etosha. However, wildebeest inhabited the wet season grazing areas when seeding of grass occurred and therefore did not appear to be drawn to the dry season grazing areas by the presence of higher levels of NFE which occurred there at seeding. The difference in percentage NFE will therefore probably not be of any great biological significance.

7.4.4.2 Crude Fibre

Although crude fibre is defined as an insoluble residue after successive boiling in dilute acid and dilute alkali (AOAC, 1965), the micro-organisms in ruminants' stomachs are able to transform cellulose into energy-producing, volatile fatty acids (Moen, 1973). Between 50 - 90 % of the crude fibre may be digestible to ruminants (Crampton and Harris, 1969), but will probably be less than 50 % in the case of dormant plants (Moen, 1973).

At Etosha, the crude fibre in grass available to

wildebeest was lowest at sprouting ($\bar{x}$ = 26,6 % ± 2,8 %), increased at seeding ($\bar{x}$ = 33,7 % ± 1,7 %) and was highest at the dormant stage ($\bar{x}$ = 34,2 % ± 2,6 %). Levels of crude fibre at seeding and dormancy did not differ significantly ($P > 0,05$) but both were much greater than the crude fibre present in sprouting grass ($P < 0,01$). There was no significant difference in crude fibre between wet and dry season grazing areas at any critical stage of growth ($P > 0,05$). Thus, crude fibre was a partly (± 50 %) digestible ingredient in the diet of Etosha's wildebeest. It constituted the second highest percentage of nutrient in the grasses, namely a yearly mean of 31,8 % from all areas. The soluble and insoluble carbohydrates formed 54,0 % and 31,8 % respectively of the DM in grass available to wildebeest at Etosha. Carbohydrates therefore totalled approximately 86 % of the grass produced. This is somewhat higher than the figure of 75 % proposed by Maynard and Loosli (1962) for edible plants, but it supports their statement that carbohydrates form the largest part of a herbivore's food supply.

7.4.4.3 Crude Protein

The factor of 6,25, used to calculate crude protein from the amount of nitrogen in the forage (AOAC, 1965), was permissible in the case of grass. This is because

nitrogen levels exceed normality (> 16 %) chiefly in oil-seed and cereal protein (Moen, 1973). Furthermore, it was not considered necessary to distinguish between crude protein and true protein in this study, since ruminants can utilise non-protein nitrogen in the forage to synthesize proteins by microbial action (Maynard and Loosli, 1962). In Section 7.4.3 I have demonstrated that the grass available to wildebeest remained above the critical level of crude protein, namely 5 %, at sprouting and seeding (Figs 7.4 and 7.5). I have also considered the effect of food selection which further enhances the intake of crude protein by the tendency which wildebeest have to select for protein-rich leaf.

At Etosha, grass available to wildebeest, predictably contained the least crude protein when dormant ($\bar{x}$ = 4,1 % $\pm$ 2,0 %). This critical nutrient increased to a peak at sprouting ($\bar{x}$ = 18,7 % $\pm$ 2,0 %) and declined again at seeding ($\bar{x}$ = 9,8 % $\pm$ 2,0 %). These differences were highly significant for the three growth stages sampled ($P < 0,01$). No significant difference in crude protein existed between wet and dry season grazing areas at dormancy and seeding ($P > 0,05$). However, at sprouting the dry season grazing areas exhibited significantly more crude protein ($\bar{x}$ = 19,7 %) than the wet season grazing areas ($\bar{x}$ = 17,8 %) at $P < 0,05$. In spite of this,

wildebeest preferred the wet season grazing areas although their crude protein level was lower. This may have been due to preference for the apparently more palatable annual grasses which predominated in the summer grazing areas (Appendix 12).

When crude protein levels exceed the amount which can be utilised by an animal, the excess is wasted through catabolism (Maynard and Loosli, 1962). It is possible that the sprouting grass available to wildebeest at Etosha provided a surplus of crude protein in both grazing areas, albeit for a brief period, which they were unable to utilise fully. Consequently, the *luxus* levels of crude protein, occurring during sprouting at dry season grazing areas, failed to attract wildebeest.

7.4.4.4 Lipid

Glycerol esters of fatty acids are the most important of the lipid group, serving as a reserve of condensed energy (Maynard and Loosli, 1962). Dormant grass available to wildebeest at Etosha contained on average 2,6 % (± 2,5 %) lipid. At seeding this was 3,6 % (± 2,2 %) and at sprouting it reached a mean maximum of 4,5 % (± 2,0 %). This increase was probably influenced by the high percentage of plant pigments which are also removed during

the ether extraction process. Sprouting grass contained significantly more lipid than dormant grass ($P < 0,02$), but no statistical differences existed between the lipid content of other growth stages. There was also no significant difference between the lipid content of dormant or sprouting grass in the wet and dry season grazing areas. However, the wet season grazing areas contained significantly higher levels of lipid at the seeding stage ($\bar{x} = 4,74$ %) than did dry season grazing areas ($\bar{x} = 2,79$ %) at $P < 0,02$. It was then that wildebeest calving was at its peak and the preference of the herds for grass high in lipid content may have favoured lactation. The advantage would, however, be marginal and it is very doubtful whether the animals could have detected this difference.

7.4.4.5 Ash

Ash content of forage only indicates the combined presence of mineral elements as a group (Maynard and Loosli, 1962) and is therefore of limited value in a proximate analysis. Furthermore, when investigating the nutritive value of forage for ruminants, quantitative determination of ash does not reflect the great variability in the type of element present. Some elements, such as silica, may even depress digestibility of the forage to ruminants (Moen, 1973).

As expected, ash content of grass at Etosha was lowest at sprouting ($\bar{x}$ = 0,12 %), higher at dormancy ($\bar{x}$ = 0,24 %) and highest at seeding ($\bar{x}$ = 0,41 %). In one instance, namely seeded grass from the Etosha Pan, a dry season grazing area for wildebeest, the ash content was 1,30 %.

7.4.5 Seasonal Relationship of Faecal Chemical Composition to Quality of Available Grass

The chemical composition of faeces from ruminants may be used as an indicator of pasture quality (Erasmus *et al.*, 1978). To test whether a relationship of this nature existed for wildebeest at Etosha, I examined the crude protein and crude fibre content of wildebeest faeces (Fig. 7.8) and the level of these two components in the grass available to wildebeest on a seasonal basis. The occurrence of important inorganic elements in the faeces was also examined.

7.4.5.1 Crude Protein

Nitrogen content of the faeces is influenced by the nitrogen content of the feed (Erasmus *et al.*, 1978). However, non-protein nitrogen (NPN) compounds are synthesized into protein by microbial action in the rumen (Moen, 1973). Furthermore, NPN, especially amides, are

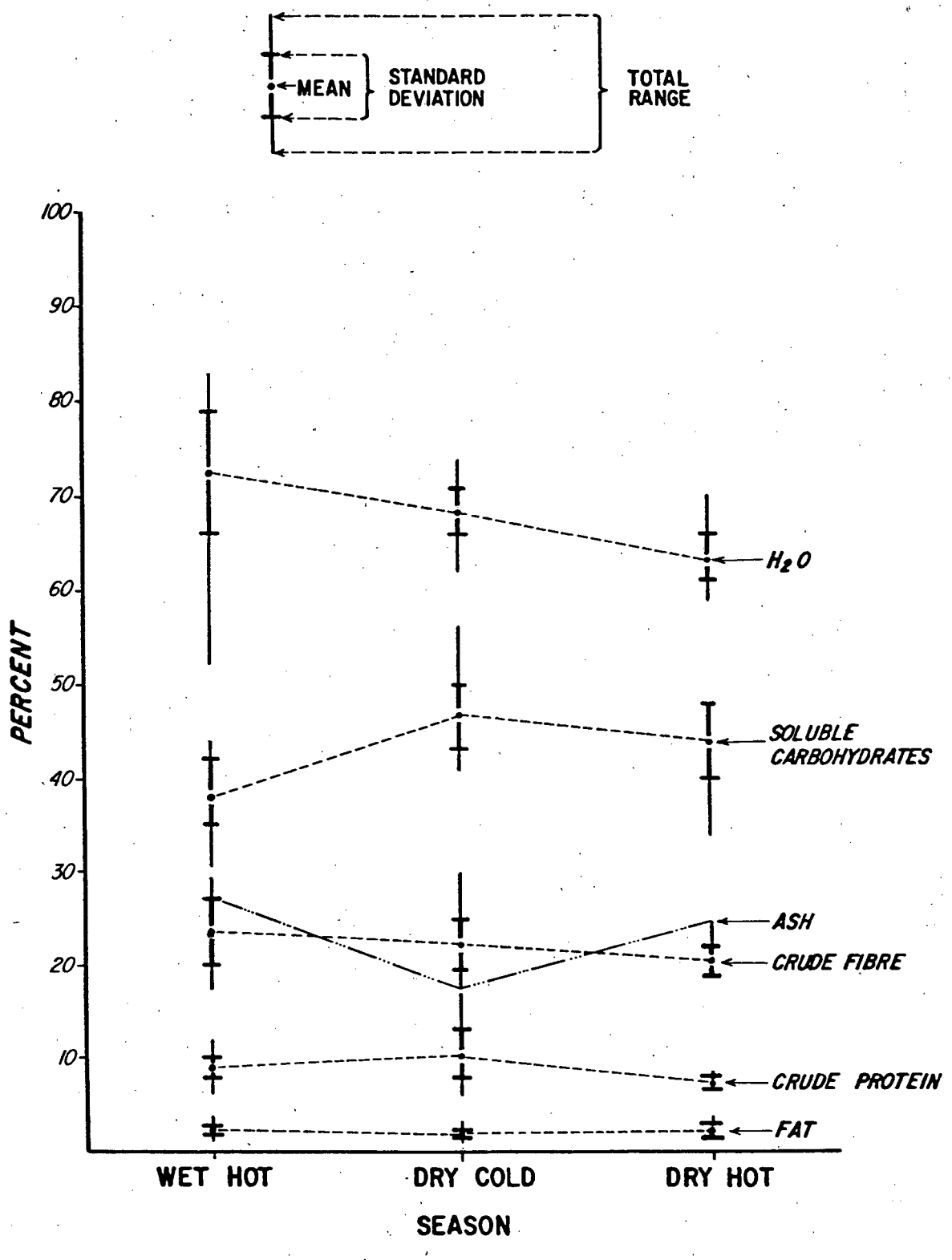

Fig. 7.8 : Chemical composition of wildebeest faeces, on a seasonal basis at Etosha (1976-78).

T-bars show standard deviation. Vertical lines show total range.

abundant in rapidly growing grass (Maynard and Loosli, 1962). Hence the high crude protein content, calculated from nitrogen of sprouting grass at Etosha (Table 7.1), may have included NPN components. For this reason, a comparison of crude protein in the faeces with that in the feed may be of limited value.

This postulation was well illustrated when faecal crude protein was compared to crude protein available in grass, on a seasonal basis. Applying the t statistic for two means, there was much more crude protein in sprouting and seeding grass ($\bar{x}$ = 13,2 %) than in the faeces of wildebeest feeding on this grass ($\bar{x}$ = 9,0 %) at $P < 0,01$. However, in dormant grass there was much less crude protein ($\bar{x}$ = 3,3 %) than in wildebeest faeces for that period ($\bar{x}$ = 10,4 %) at $P < 0,01$. Likewise, dormant grass had less crude protein than faeces samples collected in the dry, hot period ($\bar{x}$ = 3,3 % and 7,8 % respectively) at $P < 0,01$. Also, faeces samples contained significantly more crude protein in the dry, cold season than in the wet, hot season ($P < 0,05$) which is the opposite of the values obtained for grass during the same periods (Section 7.4.4.3). This may have been due to the high values obtained from five faecal samples taken on the Etosha Pan in the dry, cold season (11,9 - 16,6 %) as shown in Appendix 14. Faecal crude protein in the wet,

hot and dry, cold seasons were in both instances significantly greater than in the dry, hot season ($P < 0,02$ and $P < 0,05$ respectively).

Finally, it is tempting to speculate that the significantly higher levels of crude protein in faeces than in grass during the dry seasons may partly have been a result of wildebeest selecting relatively protein-rich leaf during this period (Section 7.3.6, Table 7.6). Nevertheless, a higher faecal crude protein level would have been expected during the wet, hot season in view of the high crude protein content of the grass during this period. However, the confounding influences of MFN urea recycling to the rumen and synthesis of protein from NPN, do not allow any definite conclusions to be drawn in this respect. These results do not agree with those of Erasmus *et al.* (1978) who found that faecal nitrogen in springbok followed the rainfall pattern.

7.4.5.2 Crude Fibre

Fibre content of springbok faeces shows seasonal variations that can be related to rainfall (Erasmus *et al.*, 1978). In the case of wildebeest, no statistically significant differences in the seasonal content of faecal crude fibre could be found ($P > 0,05$). Furthermore, no

significant differences existed between faecal crude fibre in the sexes on a seasonal basis. Faecal crude fibre analysis in wildebeest was at a much lower level than that which occurred in grass during all seasons. These differences were all highly significant ($P < 0,01$). Two reasons for this are immediately apparent. Firstly, wildebeest are selective feeders of leaf, which is low in crude fibre (Sinclair, 1974; Stanley Price, 1978). Secondly, ruminants can digest as much as 50 - 90 % of the crude fibre in their diet (Crampton and Harris, 1969), and although this ability is reduced in the dormant season, it nevertheless approaches 50 % (Moen, 1973). Thus it would appear that Etosha wildebeest are more selective feeders than the springbok investigated by Erasmus *et al.* (1978). In their discussion, mention is made of springbok grazing karroid shrubs, but quantitative data of rumen contents on a seasonal basis are not given. It should, however, be mentioned that Erasmus *et al.* (1978) used a more refined analysis of the crude fibre fraction than that employed for my investigation. This may explain, in part, our contradictory results. The results obtained from wildebeest faecal analysis, coupled to the findings on rumen contents and food selection (Sections 7.3.6 and 7.4.3) support my hypothesis that wildebeest at Etosha are able to select the food available to them very efficiently. Further proof of this proposition will be provided in the discussion of their nutritional status (Section 9).

7.4.5.3 Calcium, Phosphorus and Magnesium

In Table 7.5 the mean values and SD of calcium, phosphorus and magnesium in wildebeest faeces are given on a seasonal basis. The low sample size of three animals per season does not warrant further statistical treatment. Nevertheless, a comparison with the values found in healthy, domestic sheep was possible from investigations at present in progress at the Department of Human and Animal Physiology, University of Stellenbosch. Mean values in sheep are Ca 2,0 %; P 0,4 %; Mg 0,6 % (Belonje, 1979, pers.comm.) which compare favourably with Ca 2,51 %; P 0,3 %; Mg 0,84 % in wildebeest. Faecal excretion is the major pathway for these elements and their levels in the faeces are consequently related to their status in the animal (Maynard and Loosli, 1962). From the presently limited comparisons which could be made with healthy sheep, it appeared that the faecal levels of these three critical elements were normal in Etosha's wildebeest. However, although the analysis of wildebeest faeces reflected favourably on the level of endogenous phosphorus, it was contradicted by the findings on the circulating levels of phosphorus in the plasma as well as the levels of phosphorus in the liver, which indicated a marginal deficiency (Section 9.3). In addition, an imbalance of calcium and phosphorus in the diet could impair phosphorus

absorption and therefore invalidate this method.

7.4.6 Seasonal Faecal Production in Wildebeest and Estimates of Digestibility of Grass

To estimate these parameters in wildebeest, I used the regression equation by Coe (1980) to establish faecal production in antelope :

$$Y = \log_{10} 1{,}0841X - \log_{10} 2{,}1833$$

Where Y = kg DM faeces per 24 hours

X = live body mass in kg.

Applying this equation to the mean body mass of various classes of Etosha's wildebeest during 1978 (Appendix 20), I obtained a first approximation of the total DM faecal production by the population on a seasonal basis (Appendix 24). This is summarised in Table 7.24. The total yearly production of faeces was 1 683 222 kg which was 46,5 % of the estimated yearly intake of food (3 617 293 kg). The average digestibility of the pasture to wildebeest at Etosha would therefore be 53,5 % of the total DM food intake. This result was sufficiently close to the expected value of 55 - 60 % in a good quality feed for domestic ruminants (Reid, 1968) to provide support

Table 7.24 : Estimated seasonal faecal production in the wildebeest population at Etosha (1978)

Age-sex and social class	Dry matter faecal production by season		
	Wet, hot season (Jan. to April)	Dry, cold season (May to Aug.)	Dry, hot season (Sept. to Dec.)
Calves (0-1 yr)	98 446	97 755	79 514
Immature cows (1-2 yrs)	33 581	33 764	32 742
Immature bulls (1-2 yrs)	32 922	31 402	28 109
Sub-adult cows (2-3 yrs)	30 874	30 543	29 024
Sub-adult bulls (2-3 yrs)	25 058	23 240	20 508
Adult, non-pregnant cows	17 640	18 081	17 934
Adult, lactating and pregnant cows	183 110	181 248	182 512
Lone, territorial bulls	43 260	38 007	12 566
Adult bulls in mixed herds	24 960	25 584	25 376
Adult bulls in bachelor herds	81 259	89 717	114 486
Seasonal totals	571 110	569 341	542 771
Yearly total	1 683 222		

for using the formula suggested by F.J. van der Merwe (pers.comm., 1978) for estimating food intake (Section 7.3.9, Table 7.11). Furthermore, my estimate of digestibility of forage to wildebeest fell within the range of 50 - 62 % established for captive Red Deer by Maloiy *et al.* (1968).

7.4.7 Renal Efficiency

Plasma osmolality in wildebeest during the dry season (260 mOsm/kg) had typical mammalian characteristics. In contrast, the camel, which possesses greater adaptive abilities to survive arid environments than wildebeest, has a plasma osmolality of 340 mOsm/kg (Gordon, 1972). Plasma urea in wildebeest (6,57 mmol/l) was higher than the range of 1,0 - 4,48 mmol/l given for bovines (Belonje, 1978). Mean potassium value of wildebeest plasma (5,6 mmol/l) lay within the upper range which Belonje (1978) gives for bovines, namely 3,9 - 5,8 mmol/l. This was predictably due to the shock associated with death. Furthermore, the variation established in wildebeest (4 - 7 mmol K^+/l) corresponded well in each sample with the time elapsed from shooting to death, which ranged from instantaneous to about three minutes in the dry season. The sodium level of 138 mmol/l obtained in wildebeest plasma was well within the bovine range of 132 - 152 mmol/l (Belonje, 1978).

When the plasma : urine osmotic ratio of wildebeest was compared with that occurring in other selected mammals (Table 7.18) it appeared that wildebeest have kidneys which are approximately as efficient as bontebok and noticeably less efficient than springbok. Furthermore, the kidney efficiency of wildebeest is far lower than that of the ground squirrel at Etosha which has a theoretical maximum plasma : urine osmotic ratio of 1 : 14,9 and is specially adapted for survival under arid conditions (Marsh *et al.*, 1979). This observation on wildebeest was supported by the insignificant variation in the seasonal mean osmolality and urea of the urine (Table 7.20).

Levels of urinary potassium and sodium in the wet and dry seasons appear to be inversely related (Table 7.20). The very low sodium level of wildebeest urine in the wet season implied a low level of sodium in the diet, which was then almost exclusively green grass and rainwater. In the dry season, the high level of urinary sodium indicated an increased intake in the forage and the drinking water. A similar situation exists in the case of the ground squirrel at Etosha (Marsh *et al.*, 1979). A low urinary sodium level also indicated an extremely efficient reabsorption of sodium in the kidney. This would compensate for the chronic deficiency of Na^+, which is characteristic of herbivores (Potts and Parry, 1964).

Furthermore, the level of sodium may have influenced the level of potassium in the urine because of the differential membrane permeability of these two electrolytes (Gordon, 1972). An additional factor which could have contributed to the high level of urinary potassium in the wet season was the shock associated with the greater time lapse between shooting and death in the wet season. Wildebeest were difficult to approach for a clean, killing shot during this period and, as a result, wounded animals took longer to die. During the dry season, death by shooting occurred within about three minutes.

Based on the seasonal levels of osmolality and urea found in wildebeest urine, it appeared unlikely that they would be able to withstand prolonged periods without drinking water of suitable quality. The species' inability to significantly reduce water loss in the urine was evident in the low relative medullary thickness and consequently the low maximum plasma : urine osmotic ratio compared with mammals at Etosha such as springbok and ground squirrel. These conclusions were supported by my observations on wildebeest drinking habits which showed that water was drunk once a day by preference, occasionally once every second day, and very rarely at longer intervals.

7.4.8 Water Quality in Relation to Tolerance Levels, Kidney Efficiency, Frequency of Drinking and Grazing Patterns

The tolerance levels of wildebeest to bacteria in drinking water are unknown. However, when exposed to the high levels of bacterial occurrence in fountain water, which wildebeest preferred to drink during the dry season (Table 7.12), they were apparently tolerant. This was supported by the absence of significant pathological findings during post mortems on wildebeest (Section 10) and their visual condition rating (Section 9). The bacterial load in Etosha's water was not therefore considered to be a limiting factor.

The acceptable limits for man and domestic animals in regard to chemical quality of drinking water are based on the amount of total dissolved solids, sulphates, nitrates and fluoride present (Table 7.25). I have used these chemical elements as a standard for wildebeest. When the maximum permissible level of TDS for domestic animals was compared to mean TDS values of the different types of water at Etosha (Appendix 22), it appeared that rainwater pools, fountains and boreholes produced potable water for wildebeest. Some of the fountains favoured by wildebeest during the dry season, however, approached or

Table 7.25 : Acceptable limits of some chemical elements for water potability to mammals (according to the Standards set by the National Institute for Water Research, C.S.I.R.)

Chemical measurement	Maximum permissible level (mg/l)	
	Man	Domestic animals
TDS	3 000,0	6 000,0
SO_4	500,0	1 500,0
NO_3-N	20,0 (babies < 1 year)	110,0
Fl	2,0	6,0

exceeded the maximum permissible level for TDS (6 000 mg/l). For instance, Okondeka (No. 33, Fig. 7.3) had a TDS of 5 636 mg/l and Akomaas (No. 50) had a TDS of 6 566 mg/l. Both were heavily utilised by wildebeest. Artesian wells and the Ekuma River contained water which was not potable by domestic standards. However, I recorded wildebeest drinking from the Ekuma River at the height of the dry season (December). Water sampled at this point immediately after they had drunk, had a TDS value of 23 620 mg/l.

Mean levels of sulphate in Etosha's rainwater pools, boreholes and fountains were acceptable in all seasons, but artesian wells and the Ekuma River exceeded the maximum permissible level during the dry season. In the latter case, wildebeest drank when the sulphate level was 2 040 mg/l. Nitrates never exceeded the maximum permissible level in any water at Etosha. Similarly, fluoride remained within the limit, but reached the maximum permissible level in the Ekuma River during the wet season.

Thus the chemical quality of most water points at Etosha appeared to be generally within acceptable limits, when applying the criteria for domestic animals. However, certain water points, notably the Ekuma River, and some fountains on the western and southern edges of the Etosha

Pan which were favoured by wildebeest, exceeded the levels set for TDS and sulphates. Nevertheless, water containing a high level of TDS was utilised by wildebeest and this may have been because of their relatively efficient kidney function which resulted in a plasma : urine osmotic ratio of 1 : 5,7 (Section 7.3.12, Table 7.18). Wildebeest, however, are unlikely to be able to cope with a high level of TDS in their drinking water for prolonged periods, since the seasonal levels of osmolality found in their urine (Table 7.20), indicated that they were unable to reduce water loss significantly during the dry season.

At this point, I wish to draw attention to the fact that wildebeest showed a preference for rainwater pools above any other source of water, when they were seasonally available. Consequently, they drank rainwater almost exclusively from January to April and then subsisted largely on perennial fountains. The superior quality of seasonal rainwater pools was obvious when compared with the perennial sources of water (Table 7.14).

The relative proximity of wildebeest to water and the frequency with which they preferred to drink, normally once a day at Etosha, makes them a water-dependent species (Hofmann, 1973). Wildebeest seldom occurred more than 10 km from water at Etosha, the maximum recorded distance

being 15 km. This was in close agreement with the findings of Western (1975) who recorded that 100 % of the wildebeest in the semi-arid Amboseli region of Kenya were distributed within 10 - 12 km of water and that 90 % occurred 2 - 4 km from water. Thus wildebeest are unquestionably obligate drinkers and it has been found by Taylor (1968) that captive wildebeest had a minimum water requirement of 3,0 l/100 kg body mass.day^{-1} at 22 ^{o}C. This value rose to 4,7 litre at 22 - 40 ^{o}C (12 h at 22 ^{o}C and 12 h at 40 ^{o}C). At Etosha, I observed that daily drinking was preferred, by following marked wildebeest from sunrise to sunset, for periods of up to 14 hours (Section 4). Out of 46 marked wildebeest, 43 (94 %) drank water on a daily basis and three drank at an interval of two days. Under exceptional circumstances, such as when predators occupied a waterhole for lengthy periods, wildebeest which were prevented from drinking for two days moved to alternative waterholes.

In turn, the daily drinking habit of wildebeest at Etosha imposed restrictions on their grazing patterns. In this regard water was considered to be a factor which limited the ability of the species to forage beyond a radius of more than 15 km from a drinking point. Thus, the highly seasonal nature of water distribution at Etosha resulted in a corresponding apportionment of the wildebeest population. Consequently, "wet season dispersal areas"

and "dry season concentration areas" (Bigalke, 1961; Western, 1975) have developed. The significance of this became apparent when it was considered that for approximately four months of the year (January to April) rainwater pools were usually abundant and wildebeest could forage over the entire open grassveld areas of Etosha. However, with the drying of these ephemeral pools, a period of up to eight months commenced which confined the wildebeest to a greatly decreased foraging range. This water dependence may be limiting to the wildebeest population during a dry climatic cycle and I will discuss the broader implications of this water-forage link when reviewing the nutritional balance of wildebeest and their food competitors (Section 8).

7.4.9 Milk Quality and Growth Rate of Calves

The composition of milk taken from wildebeest at Etosha (Table 7.16) compared favourably with the means given for 12 species of Artiodactyla from tropical areas (A. Smith, 1970), in regard to fat and lactose. Etosha wildebeest milk contained 10,66 % fat and 4,82 % lactose, whilst tropical Artiodactyla have milk values of 10,4 % fat and 4,0 % carbohydrates (A. Smith, 1970). However, the protein content of Etosha wildebeest milk was 5,6 % which was somewhat lower than the mean value of 7,9 % in tropical

Artiodactyla (A. Smith, 1970). Nevertheless, wildebeest milk was considerably richer than domestic cows' milk which contains 3,7 % fat, 3,1 % protein and 4,9 % lactose (Maynard and Loosli, 1962). A high level of milk fat and protein results in an increase in the amount of energy available to the calf and this was reflected in the gross energy value of wildebeest milk (6,14 $J.g^{-1}$ fluid milk) compared to the equivalent value of domestic cows' milk (2,91 $J.g^{-1}$ fluid milk). Consequently, wildebeest calves had access to a high energy diet which was reflected in their growth rate. In the present study I estimated calf growth at 84 kg (230 $g.day^{-1}$) in the first year (Section 5.3.3, Table 5.7). This compared well with the estimates for wildebeest calves of 247 $g.day^{-1}$ (Braack, 1973) and 242 $g.day^{-1}$ (Attwell, 1977). Furthermore, by measuring calves shot for veterinary investigation at Etosha (Section 10), the time taken to double the birth mass was estimated to be 50 days. This was similar to the findings of Watson (1967) in Serengeti wildebeest and also similar to domestic calves, where birth mass is doubled at 47 days (Bunge, as quoted by A. Smith, 1970). Considering the higher energy and protein values in wildebeest milk, the prediction would be more rapid gain in body mass than for domestic calves. However, wildebeest calves are more active than domestic calves because of the demands made by free existence. This increased activity may have accounted

for a reduced gain in body mass. Nevertheless, wildebeest calves grow at a prodigious rate when compared to human infants which, having access to 1,6 % protein in the mother's milk, take 180 days to double their birth mass (Bunge, as quoted by A. Smith, 1970).

An increase in percentages of the energy-rich fat and protein components of wildebeest milk also resulted in a corresponding reduction in the water content of the milk. For example, domestic cows' milk contains 87 % water (Maynard and Loosli, 1962), whereas wildebeest milk may have contained less than 78 % water, if allowance was made for all the dissolved constituents. Thereby, water requirements of the nursing wildebeest cow would be favourably reduced.

7.5 SUMMARY

7.5.1

Nutrition in wildebeest was investigated by examining the quantity and quality of grass available to them, as well as their faecal production. In addition, rumen contents were examined and the drinking habits of wildebeest at Etosha were related to their kidney efficiency and urine

composition. Quality of drinking water and milk composition were also considered.

7.5.2

From examination of rumen contents on a seasonal basis, it was found that at least 96,5 % of the diet of wildebeest consisted of grass. Furthermore, they selected protein-rich grass leaf and sheath during the wet season when these two components made up 75,4 % of their diet. Reduced availability, especially of grass leaf during the dry season, forced wildebeest to feed largely on less nutritious grass stems which then comprised 61,5 % of the diet, compared to only 14,1 % in the wet season.

7.5.3

Proximate analyses of the effects of area, season, and growth stage of grass foraged by wildebeest showed a high mean level of protein (17,7 %) during the sprouting stage in January. This decreased to 10,7 % at seeding and 4,1 % at dormancy. The other two major constituents in the food which fluctuated correspondingly were soluble carbohydrates and crude fibre. The moisture content of freshly harvested grass declined from 74 % at the sprouting stage to 58 % during seeding and only 5 % at dormancy. These decreasing levels of moisture in the

forage corresponded with the highly seasonal rainfall at Etosha and the reduced availability of drinking water.

7.5.4

Measurement of the gross energy values of grass from areas inhabited by wildebeest allowed for an estimation of the metabolisable energy available to wildebeest. Mean ME was 11,49 $MJ.kg^{-1}$. When this estimate was coupled to the production of the grasslands, an estimate was obtained of the maximum and residual amounts of usable energy produced. Similarly, an estimation of the maximum and residual production of crude protein by the grasslands was possible. These data were necessary to measure whether the supply of energy and protein was sufficient to meet the demand by the large herbivores inhabiting the grasslands of Etosha (Section 8).

7.5.5

Dry matter food intake by the wildebeest population was estimated on a seasonal basis, using various equations based on domestic cattle, and taking into account the seasonally changing age-sex and social classes. In this manner it was estimated that, on average, a population of 2 269 wildebeest would require 3 617 tons dry matter forage annually. This was equivalent of 1,58 tons DM $forage.year^{-1}$ per individual or 4,36 kg DM $forage.day^{-1}$ per individual.

7.5.6

Comparison of the quality of grass with that of other areas revealed that Etosha's grass contained more than twice the percentage of crude protein during the wet season than other areas in Africa which were inhabited by wildebeest (13,9 % as compared to 5,7 %). In the dry season, Etosha's grass contained 4,1 % crude protein whilst the other areas had a mean value of 3,7 %.

7.5.7

The minimum crude protein requirements of wildebeest were considered, taking into account the favourable influence of food selection incurred by their manner of feeding. When an arbitrary minimum level of 5 % crude protein was applied to the seasonal situation at Etosha, it was evident that a surplus of this critical nutrient was available to wildebeest during four months of the year, namely the wet season from January through April. Thereafter the level of crude protein in grass declined significantly during dry season dormancy to below the minimum level required. However, the ability of wildebeest to synthesize protein, by microbial action in the rumen and by recycling of urea in the saliva, probably compensated for this seasonal shortfall of protein.

7.5.8

No shortage of highly digestible energy in the grass available to wildebeest at Etosha could be found during the seasonal year. This was due to a soluble carbohydrate content of 46 - 61 % plus the fact that at least 50 % of the crude fibre which was present at levels of 27 - 34 %, may have been utilised by microbial action in the rumen. This ability to transform non-digestible cellulose into energy-producing fatty acids, would further ensure the energy supply to a ruminant such as wildebeest.

7.5.9

There was no significant seasonal relationship between the quality of grass and the crude protein and fibre composition of wildebeest faeces. This contradicted earlier investigations on springbok, and may have been influenced by the wildebeest's ability to select for protein-rich grass leaf plus the fact that the proximate analysis used in this investigation was less refined than that used in other studies.

7.5.10

An estimation of the yearly faecal production by a mean population of 2 269 wildebeest was 1 683 tons dry matter,

which indicated that the digestibility of Etosha's grass to wildebeest was 53,5 %. This result, which was similar to the normal digestibility values of 55 - 61 % for domestic ruminant feeds, confirmed that the estimation of food intake by the wildebeest population was within acceptable limits.

7.5.11

Water quality in boreholes, artesian wells, fountains, rainwater pools and a river was evaluated on a seasonal basis for bacteria, macro-elements and trace elements. At most sampling points, dry season bacterial counts were higher than wet season counts and fountains had a higher incidence of bacteria than boreholes. Similarly, fountain water contained a higher level of chemicals and was more alkaline than borehole water. All water sources improved in quality in the wet season compared to the dry season. Wildebeest favoured natural fountains in the dry season and drank exclusively from rainwater pools in the wet season. Water quality at Etosha was, in most cases, within the maximum permissible chemical levels set for domestic animals. Instances were recorded, however, where wildebeest drank from river water containing levels of total dissolved solids which were four times higher than the maximum permissible level and where the sulphate

level would have been unacceptable for domestic stock. Bacteria, which occurred at a high level in the fountain water favoured by wildebeest, did not appear to affect the species detrimentally. Wildebeest were found to be obligate drinkers, requiring water on a daily basis during 94 % of observations. They rarely went without drinking for more than two days. An important fact which emerged during the study was that the wildebeest population was confined to a maximum recorded radius of 15 km from drinking water during the dry season. This imposed restrictions on their ability to forage beyond a certain range at a time of year when the grazing quality was at its poorest.

7.5.12

Kidney efficiency was determined by relating medulla thickness to kidney size. It was evident that wildebeest possess a kidney which equals that of the bontebok in efficiency, but is less efficient than the kidney of springbok. This prediction was supported by the maximum plasma : urine osmotic ratio of 1 : 5,7 (cf. 1 : 5,4 for bontebok and 1 : 8,3 for springbok). Furthermore, wildebeest appeared to be unable to reduce water loss very significantly via their urine which is reflected in small seasonal differences found in urine osmolality.

Faecal water loss remained high during all seasons of the year.

7.5.13

Wildebeest milk was found to be a source of high energy for the precocious calf, because of its high levels of fat and protein which greatly exceeded those of a dairy cow. Gross energy value of wildebeest milk was 6,14 $J.g^{-1}$ compared to 2,91 $J.g^{-1}$ in dairy milk. The resultant growth of calves was rapid, doubling their birth mass at 50 days, in spite of their very active nature which may have placed a restraint on growth.

7.5.14

When the relative quality of the forage, the moisture content in the forage, and the availability of drinking water were considered, it was apparent that Etosha's wildebeest existed under ideal conditions in regard to these critical factors for about four months of the year, namely the wet season which occupied January through April. For the remaining eight months' dry season they experienced increasing difficulty in obtaining good quality food because of their restriction to perennial water sources. Nevertheless, in years of average and above average rainfall, which were experienced during the

present study, it appeared unlikely that nutrition was a limiting factor to the population. In a dry cycle, which occurs periodically at Etosha, nutrition may, however, prove limiting. This aspect is discussed in detail in Section 8.